# On the Anaspidacea, Living and Fossil.

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With Plates 11 & 12 and 62 Text-figures.

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# 1. HISTORICAL INTRODUCTION.

THE first members of the Anaspidacea to be discovered and described were certain fossil forms occurring in the Permian and Carboniferous strata of Europe and North America, and it was not until long afterwards that a living representative was found in the fresh waters of Tasmania and recognised as the near relative of these very ancient fossils.

In 1856 Jordan and von Meyer (1) described a fossil shrimp from the Permo-Carboniferous of Saarbrück which they named Gampsonyx fimbriatus, and which was seen to combine certain features of the Podopthalmate Crustacea with the entire absence of a carapace.

In 1865 and 1868 Meek and Worthen (2 and 3) figured two similar forms from the Coal-measures of Illinois which they named Acanthotelson stimpsoni and Palæocaris typus.

The systematic position of these fossils remained obscure until Packard re-examined them, and in a series of papers (4, 5 and 6) did a good deal to elucidate their structure and affinities. He instituted the use of the term "Syncarida" to include the three genera and to designate a group of the higher Crustacea intermediate in its characters between the Schizopoda and the Edriopthalmata. Packard's conception of the affinities of this group have been borne out by recent investigations, and his name "Syncarida" has been adopted by Calman as one of the divisions of the Malacostraca.

In 1893 Thomson (7) gave an account of a remarkable freshwater shrimp from the top of Mount Wellington, Tasmania, which was pointed out to him by Mr. Rodway, of Hobart, and which had been known to, and even occasionally eaten by, the settlers for some time. Thomson named the animal An aspides tasmaniæ, described the most important points of its external anatomy, and decided that it belonged to the sub-order Schizopoda, of which he considered it the most primitive member.

The connection between Anaspides and the fossil Syncarida was first pointed out by Calman (8), who revised Thomson's description in certain particulars, and drew a careful comparison between Anaspides and the Carboni-

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ferous fossils, concluding therefrom that they all belonged to the same order and are very closely allied.

In a subsequent paper (9) the same author amplifies and crystallises the views of Boas and Hansen on the classification of the Malacostraca, and proposes to do away with the order Schizopoda and to redistribute its component families, uniting the Euphausiidæ with the Decapoda to form a division Eucarida, while the Eucopiidæ, Lophogastridæ and Mysidæ are united with the Cumacea, Amphipoda and Isopoda as Peracarida. The Anaspididæ are placed in a separate subdivision, the Syncarida, together with the three fossil forms mentioned above.

Calman gives the following diagnosis of the three divisions:

Division Eucarida.—Carapace coalescing dorsally with all the thoracic somites. Eyes pedunculate. Antennal protopodite with, at most, two distinct segments. Mandible without lacinia mobilis in adult. Thoracic limbs flexed between fourth and fifth segments. No oostegites. An appendix interna sometimes present on pleopods. Hepatic cæca much ramified. Heart abbreviated, thoracic. Spermatozoa spherical or vesicular, often with radiating appendages. Development, as a rule, with metamorphosis.

Division Peracarida.—Carapace, when present, leaving at least four thoracic segments distinct. First thoracic segment always fused with the head. Antennal protopodite typically of three segments. Mandible with lacinia mobilis (except in parasitic and other modified forms). Thoracic limbs flexed between fifth and sixth segments. Oostegites attached to some or all of the thoracic limbs in female, forming a brood-pouch. No appendix interna on pleopods. Hepatic cæca few and simple. Heart elongated, extending through the greater part of the thoracic region, or displaced into abdomen. Spermatozoa filiform. Development taking place within brood-pouch; young set free at a late stage.

Division Syncarida.—Carapace absent. All the thoracic segments distinct. Eyes pedunculate. Antennal protopodite of two segments. Mandible without lacinia mobilis. Thoracic

limbs flexed between fifth and sixth segments. No oostegites. No appendix interna on pleopods. Hepatic cæca numerous. Heart elongated, tubular.

Largely as the result of Calman's writings, the importance of Anaspides, both as the sole survivor of a group of Crustacea, otherwise known only from the Permo-Carboniferous seas of the northern hemisphere, and as the representative of probably the most primitive Malacostracan division, became obvious, so that it was clearly desirable to learn more about its habits and internal anatomy, and to find out if other allied forms were still existing in the freshwaters of the southern hemisphere.

In the autumn of 1907, at the suggestion and through the assistance of Professor G. C. Bourne, I went to Tasmania to investigate Anaspides. On arriving in Melbourne I met Mr. O. A. Sayce, of Melbourne University, and learnt that a few weeks before my arrival he had obtained some specimens of a freshwater Crustacean, which he believed to be closely related to Anaspides, from a small stream to the west of Mr. Savce has subsequently published an Melhourne. account of the animal, which he calls Koonunga cursor (10 and 11), belonging to a separate family, Koonungidæ of the Anaspidacea. Perhaps the most interesting point about this animal is the fact that, unlike Anaspides and all other Schizopods, it possesses sessile eves, a characteristic which tends to break down the old distinction between Podopthalmata and Edriophthalmata, a distinction which Calman's classification also ignores.

My own investigations in Tasmania were directed chiefly towards the elucidation of the obscure points in the habits and internal anatomy of Anaspides tasmaniæ, and a preliminary account (12) of these matters was published on my return in June, 1908. I was also able to report the discovery of a new species and genus of the Anaspididæ, Paranaspides lacustris, from the great Lake of Tasmania. As a result of my studies 1 inclined to the conclusion that the Anaspidacea, while possessing many peculiar features, were

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related by certain characters—e.g. filiform spermatozoa and the structure of the heart—to the Peracarida, and by others to the Decapoda, a conclusion which has been subsequently confirmed. The composite character of the Anaspidacea, which seem to be constructed by uniting characteristics taken from the other divisions of the Malacostraca, appeared to me to point to the extremely primitive nature of the group, and to confirm Calman's opinion that they should be separated from the other Malacostracan divisions as a discrete group, the Syncarida.

In the September number of the 'Geological Magazine' for 1908, Dr. Henry Woodward (13) describes for the first time some specimens of a fossil crustacean from the Coal-measures near Ilkeston, Derbyshire, which must be considered as the most perfectly preserved specimens of fossil Syncarida that have as yet been found. Dr. Woodward names them Præanaspides præcursor, and there can be no doubt that they represent an exceedingly close ally of the living Anaspidacea. The details of segmentation, of the form of the limbs, and the general posture of the body in Præan aspides are exactly reproduced in the living Anaspides or Koonunga, and we are amply justified in placing this ancient palæozoic fossil together with the living genera in the same order or even in a nearer relationship (text-fig. 3).

Our knowledge therefore of this interesting group of primitive Crustacea is beginning to take definite shape, and since in the future it must always hold a prominent position in Crustacean morphology and classification, it is, perhaps, timely to bring together all we know about these animals in a systematic form, and to attempt to determine their place in classification, and the light which they throw upon the evolution of the higher Crustacea.

Before leaving the historical aspect of our subject, reference must be made to Professor Fritsch's views upon the affinities of the fossils which he has described (17), from the carboniferons strata of Bohemia. In his admirable memoir he describes a fossil Malacostracan, Gasocaris

Krejcii, which he places together with Gampsonyx, Palæocaris, Acanthotelson and Mectotelson in a sub-order of the Podopthalmata, which he names Simplicipoda. Professor Fritsch believes that Gasocaris had simple uniramous thoracic limbs, and he also ascribes this character to the other genera, despite Packard's assertion in regard to Palæocaris, and the apparent condition of Gampsonyx. Professor Fritsch denies that any of these forms is related to Anaspides, or to any other Schizopod. on the ground of their possessing uniramous limbs. As Calman (18) has pointed out, the mere fact, if it were established, that some of these fossil forms had uniramous limbs would not invalidate the conclusion that they are related to Anaspides. This relationship is established more effectively by such common characters as the lack of a carapace, the eight free thoracic segments, the pedunculated eyes and form of the antennæ, tail-fan and telson. With regard to the possession of biramous limbs, we know now that Præanaspides exhibited this character, and the same is true of Palæocaris and perhaps of Gampsonyx. It must also be remembered that the exopodites of the thoracic limbs in Anaspides and its living allies are exceedingly slender and delicate structures, and that even in the beautifully preserved fossil Præanaspides they are by no means easy to be made out, though they are demonstrably present. We cannot therefore attach great weight to Professor Fritsch's assertion that they are altogether absent in Gasocaris and Gampsonyx, and even if this is the case, it would not alter our conviction that these forms are closely related to Anaspides. The fossil, Gasocaris (see text-figs. 59, 60, 61), the details of whose structure Professor Fritsch so beautifully illustrates, reproduces with great exactitude the essential features of Anaspides. The pedunculated eyes, the first antennæ with three jointed peduncles, the second antennæ with their scales, the entire absence of a carapace, the form of the telson and tail-fan, are all nearly identical with the corresponding features in Anaspides.

With regard to the segmentation of the body, Professor Fritsch confesses that he is doubtful, but the number of segments which he gives in his restored figure is plainly wrong. He only figures six thoracic segments in the restored figure, but it appears to be demonstrable from his figure of an actual specimen in ventral view that there are eight free thoracic segments carrying eight similar limbs. It is impossible not to observe that if only Professor Fritsch, at the time of writing, had been familiar with the living Anaspides, he would have interpreted his fossils otherwise. But what shall we say of the restoration of Gampsonyx, in which, according to Professor Fritsch, there were seven abdominal somites besides the telson, and two pairs of maxillipeds in front of the seven pairs of thoracic legs? As Calman points out, these characters are so exceedingly peculiar as to preclude direct comparison with any other known Crustacean, and would remove Gampsonyx from any immediate relationship to the Malacostraca at all. While gratefully acknowledging, therefore, Professor Fritsch's careful descriptions of these interesting fossils, we find it impossible to follow him in his general restorations of them, or in his denial of their relationship to the Anaspidacea. There is one other point in Professor Fritsch's work which may excite a comment, and that is the alleged presence of an otocyst on the inner ramus of the uropod in Gasocaris and Gampsonyx. An otocyst in this position is only found elsewhere among the Mysidacea; it is not present in the living Anaspidacea or in Præanaspides.

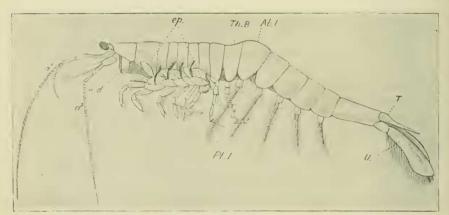
### 2. EXTERNAL MORPHOLOGY.

(A) General Appearance.

The Syncarida are rather small animals, the largest size being attained by the living Anaspides tasmaniæ, exceptional specimens of which may measure over two inches in length. The smallest form known is the living Koonunga cursor, which measures about a quarter of an inch in length.

We may describe, as a type, the general appearance of A. tasmaniæ, the mountain-shrimp of Tasmania, found in the pools of rivers and in tarns at a high elevation. The chitinous integument is soft and uncalcified, and of a strawyellow colour; beneath it in the skin are numerous branching black chromatophores, arranged in a similar pattern on each segment. Along the dorsal middle line two dark lines are visible, which are caused by the pigmentation on the floor of the pericardium.

In the natural position the body is held straight and un-



Text-fig. 1.

Paranaspides lacustris,  $\mathcal{Q}$ . Lateral view.  $\times 4$ .  $u^1$ . First antenna.  $u^2$ . Second antenna. md. Mandible. cp. Gills. Th. 8. Eighth thoracic segment. Ab. 1. First abdominal segment. Pl. 1. Eirst abdominal appendages. T. Telson. U. Uropod.

flexed with the limbs disposed in the characteristic manner shown in Pl. 11, fig. 1. The normal habit of the animal is to walk or run upon the stones at the sides or bottom of the deep pools in which it lives; this walking movement is effected by the endopodites of the eight thoracic limbs, but it is also assisted by the long exopodites of the abdominal appendages. The exopodites of the thoracic limbs are kept in a continual waving motion, and no doubt aid in respiration by agitating

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the water round the delicate leaf-like external gills attached to the bases of the thoracic limbs.

The body consists of a head, bearing a pair of pedunculated eyes, and there follow apparently eight free thoracic segments, six abdominal segments and a telson. The sixth abdominal segment carries a pair of expanded, backwardly directed pleopods, which form a powerful tail-fan.

Paranaspides lacustris (text-fig. 1, and Pl. 11, fig. 2), from the Great Lake of Tasmania, although in its detailed

### TEXT-FIG ?

2. × 16 8

Koonunga cursor, J. from a drawing by Mr. Sayce.  $\times$  16.

structure very similar to Anaspides, differs very widely from it in external appearance, and in this respect it is probably the most aberrant of all the Syncarida, including the fossil forms. The body, instead of being deeply pigmented, is of a transparent green colour, sparsely powdered with black dots; and there is a very marked dorsal flexure. The abdomen is elongated, the tail-fan enlarged, the exopoditic scales of the second antennæ also enlarged, and the eyes are borne on elongated stalks. All these characters, which differentiate Paranaspides from the other Anaspidacea, are correlated with the habits of the animal, which

lives among weeds in the littoral region of the lake, rather after the manner of a prawn, and pursues more of a swimming habit than the rest of the order to which it belongs. This habit and the characters correlated with it are therefore most probably a fairly recent acquisition.

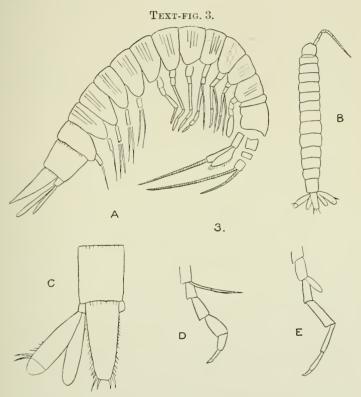
The other living representative, Koonunga cursor, is a little marbled-grey animal which differs from Anaspides in several important characters, such as the possession of sessile in place of stalked eyes, the entire absence of a scale on the second antennæ, and the presence of only seven free thoracic segments, but it closely resembles Anaspides in general appearance, especially in its habit of running with the body held straight and unflexed.

Of the fossil forms we can say for certain that they followed a similar mode of life to Anaspides and Koonunga. There is no trace in any of them of a true dorsal flexure, the fossils being in many cases preserved with the body quite straight as in the normal walking position of Anaspides. The tail-fan is small, the external scales not enlarged, and the eyes either shortly pedunculated or possibly in some cases absent.

The most perfect resemblance to Anaspides is afforded by the English carboniferous fossil Praeanaspides, described by Woodward. The segmentation and posture of the body, the detailed jointing of the limbs and antennæ in this fossil so exactly reproduce the corresponding features of the living Anaspides, that so far from there being any doubt as to the two forms being referable to the same order, it is justifiable to include them in the same family. The entire absence of the characteristic leaf-like gills in this and all the other fossil Syncarida is unfortunate, but we could hardly hope that these extremely delicate and perishable structures should be preserved for us in a fossil state.

With regard to the other fossils, although there can be small doubt that we are dealing with allied forms, it is difficult to be certain about details. Gampsonyx (text-fig. 53) has a very similar body form and segmentation to Anaspidos,

and apparently some of the thoracic limbs were biramous. The first thoracic limb was, however, raptorial and greatly enlarged. There is less doubt about Palæocaris (text-figs. 56, 57), as the thoracic limbs are distinctly biramous, there



Præanaspides præcursor, after Henry Woodward. A. Lateral view. B. Dorsal view. C. Telson and uropods. D. Fourth thoracic limb. E. Seventh thoracic limb,

are eight free thoracic segments, and the antennæ and tailfan are very similar to those structures in Anaspides. The eyes are unfortunately unknown.

Gasocaris (text-fig. 59), despite Professor Fritsch's assertion that the limbs are uniramous, was certainly a typical member of the Anaspidacea in all other respects.

A can thotelson (text-fig. 62) appears to me to occupy a different position, and I am doubtful if it is rightly associated with the Syncarida at all. The thorax only possessed seven free segments, and the thoracic limbs show no trace of being biramous. The abdominal limbs are expanded, flabellate structures, and the tail-fan is elongated and sharply pointed. The only resemblance of this creature to the Syncarida is the very general feature that a carapace is absent, and there is really no reason for supposing that this fossil is not a generalised Amphipod. The condition of the eyes is mknown.

# (B) Segmentation.

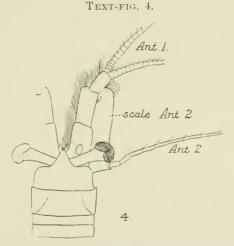
Perhaps the most striking feature of the Anaspidacea is the entire absence of a carapace. In Anaspides tasmaniæ there appear to be eight free thoracic segments and there are undoubtedly six abdominal segments, without counting the telson. The true segmental value of the first thoracic segment behind the head has, however, been called in question by Calman (8). He inclines to the view that the groove separating the head from what appears to be the first segment corresponds to the cervical suture in the Decapeda, and that the apparent segment behind this suture really represents three segments belonging to the two pairs of maxillæ and the first thoracic limbs. The compound nature of the segment is possibly indicated by the definite lateral suture which crosses it on each side in the position shown in text-figs. 1 and 4.

Whether this anterior segment represents three fused segments or not, a question which may remain open to doubt, it is certain that its freedom from the head is far more complete in Anaspides than in any of the higher Malacostraca, and that the process of cephalisation has not gone so far in Anaspides as in the latter. Since, also, there is no doubt that the first thoracic segment is incorporated in, though it may not entirely represent, this segment, we will speak of it as the first thoracic segment.

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The segmentation of Paranaspides corresponds exactly with that of Anaspides, but in Koonunga cursor there are only seven free thoracic segments, the anterior segment bearing the first thoracic limbs being definitely fused with the head, so that the segmentation agrees with the condition in the more primitive Amphipoda and Isopoda.

Among the fossil Anaspidacea we meet with an interesting condition. In Præanaspides there are seven large thoracic segments, and an extremely narrow segment in front, sepa-

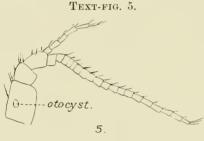


Paranaspides lacustris. Head with first and second antenna in situ.

rated from the head by a distinct groove (text-fig. 3). In Palæocaris, Gampsonyx, and probably Gasocaris there are also eight thoracic segments, the most anterior segment behind the head being narrow as in Præanaspides. The extreme narrowness of this segment suggests that it really does represent the single first thoracic segment which in Anaspides has invaded the head-region, and finally in Koonunga has become fused definitely with the head. Behind this rather problematical first segment the segmentation of the body agrees perfectly in all the Anaspidacea, both living and fossil. There is no trace of an extra segment in the posterior part of the thorax, which has been supposed to be present in the Euphansiidæ.

(c) Appendages.

The first antennæ in all the Syncarida present a very uniform structure; there is a three-jointed peduncle with two flagella attached. In all the living forms, and probably in Præan aspides, there is a definite flexure between the second and third joints; this flexure does not appear in the fossil Gampsonyx and Palæocaris. In all forms, except apparently Gampsonyx, the inner flagellum is very much



Koonunga cursor. First antenna.

shorter than the outer; in Gampsonyx the two flagella appear to have been of equal length.

In all the living forms an auditory organ has been discovered upon the upper surface of the basal joint of the peduncle of the first antenna. This organ is roughly oval in Paranaspides and Koonunga, kidney-shaped in Anaspides.

It consists of a hollow sac opening on the dorsal inner surface of the basal joint of the first antenna by a narrow transverse slit. The hollow of the sac is filled with fluid, but there are no solid concretions of any kind. On the outer wall of the sac is a row of club-shaped chitinous rods, arranged in a single antero-posterior series. If we study the histology of the sac by means of a transverse series (Pl. 12, fig. 1) we see

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that the club-shaped rods are fixed into hollow sockets by means of a pedicel which is continuous into one of the columnar cells which form the outer wall of the otocyst. From these cells muscular strands pass outwards and are connected with the pigmented ectodermal cells upon the outermost wall of the antenna. The internal chitinous wall of the otocyst is furnished with short tooth-like setæ. Below these setæ are flattened cells which come into connection with fine nervous processes sent out from the nerve of the first antenna.

TEXT-FIG. 6.

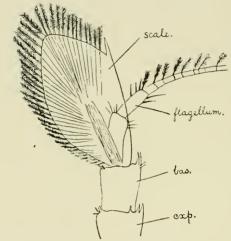
Anaspides tasmaniæ. Second antenna.

The way in which this otocyst functions is not very obvious. It is clear that the club-shaped rods are not the final sense elements since they are not connected directly with the nerve-endings. The final sense elements are evidently represented by the short setæ on the internal wall, which have not been hitherto observed. It appears, therefore, that the club-shaped rods transmit the stimulus through the fluid of the sac to the sensory setæ on the internal wall and so to the nerve. The muscular apparatus connecting the club-shaped rods with the external ectoderm suggests that the original stimulus comes from the exterior, and

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impinges on the ectodermal cells of the antenna, then that these transmit the stimulus to the muscles which pull upon



TEXT-FIG. 7.

Paranaspides lacustris. Second antenna. bas. Basipodite.] cxp. Coxopodite.

TEXT-FIG. S.

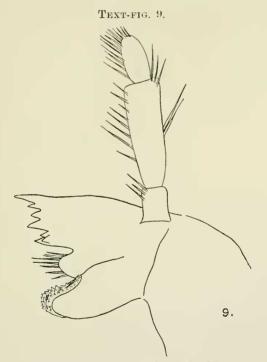
Koonunga cursor. Second antenna.

the club-shaped rods. These in their turn transmit the impulse to the setæ and so to the nerve.

If this interpretation is correct the otocyst of the Anaspi-

dacea, although agreeing essentially with that of the Decapoda, differs from the latter in responding to stimuli from the external world, as well as to internal stimuli set on foot by the position of orientation.

The second antennæ consist of a two-jointed protopodite, which supports an exopoditic scale and a flagellate endopodite. The scale is comparatively small in Anaspides (text-fig. 6)



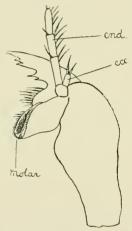
Anaspides tasmaniæ. Mandible.

and the fossil forms; it is considerably enlarged in Paranaspides (text-fig. 7), probably in correlation with the swimming habit, and is altogether absent in Koonunga (text-fig. 8). The typical form of this antenna with its exopoditic scale and flagellum is characteristic of the "Schizopoda" and Decapoda.

The mandible in Anaspides tasmaniæ (text-fig. 9)

has the biting face divided into three regions-an upper toothed portion, which differs slightly in the right and left mandible, a lobe bearing a row of spines, and a lower molar surface. The lacinia mobilis, characteristic of the Peracarida, The palp is three-jointed. The mandible of is absent. Paranaspides lacustris (text-fig. 10) has the same structure as the above, but the palp has a peculiar formation, which is particularly well marked in old specimens. In old specimens it appears to be distinctly four-jointed, and the basal joint carries a very definite, little, external branch

TEXT-FIG. 10.



Paranaspides lacustris. Mandible.

tipped with two setæ. In young specimens the extra joint, i.e. between segment two and three, may be absent, and the external branch is not so conspicuous. The external branch occupies the position of an exopodite, and if the mandibular palp in this form is really biramous, it would be unparalleled in Crustacea except among the Copepoda and Ostracoda. Considering, however, that Paranaspides is otherwise a rather specialised form, and that the character in question is best marked in old specimens, it seems doubtful if we are really dealing with a primitive characteristic.

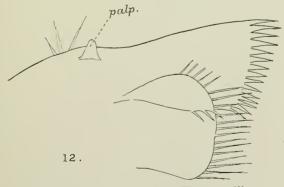
The mandible of Koonunga (text-fig. 11) possesses a toothed ridge and a single lobe beneath it bearing short TEXT-FIG. 11.



Koonunga cursor. Mandible.

spines and a few small papillæ. Sayce regards this lower lobe as the molar surface, the spine row being, according to

TEXT-FIG. 12.

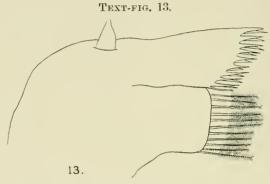


Anaspides tasmaniæ. First maxilla.

him, absent, but since the molar surface is not normally furnished with setæ in this manner, it seems better to regard

the lower lobe as corresponding to the spine row of the other forms. The palp is three-jointed, with a very short termina joint.

Apart from the abnormal condition of Koonunga, the



Paranaspides lacustris. First maxilla.

mandible of the Anaspidacea resembles that of the Mysidacea, except that the lacinia mobilis, characteristic of the latter, is absent in the former.

In the Euphausiacea and Decapoda the mandible consists

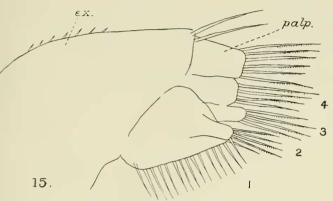
TEXT-FIG. 14.

palp. 14.

Koonunga cursor. First maxilla.

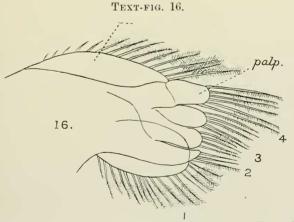
of biting lobe and molar surface without any spine row or lacinia mobilis. The Anaspidacean mandible is therefore intermediate in structure between that of the Peracarida and Eucarida.

The first maxilla of Anaspides (text-fig. 12) consists of two biting blades, the upper one armed with stiff spines, the



TEXT-FIG. 15.

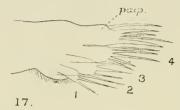
Anaspides tasmaniæ. Second maxilla. ex. Exopodite. 1, 2, 3, 4. Gnathobasic lobes.



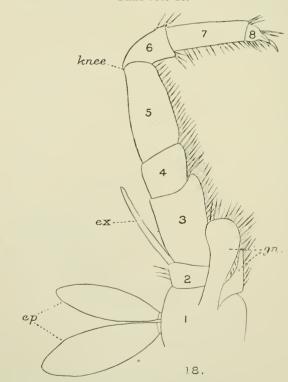
Paranaspides lacustris. Second maxilla. ex. Exopodite 1, 2, 3, 4. Gnathobasic lobes.

lower with plumose setæ; a palp is present in the form of a small conical tubercle. In Paranaspides the structure is essentially similar, but the palp is rather more conspicuous. In

# Text-fig. 17.



Koonunga cursor. Second maxilla. ex. Exopodite. 1, 2, 3, 4. Gnathobasic lobes.



Anaspides tasmaniæ. First thoracic limb. ep. Gills ex.Exopodite. gn. Gnathobasic lobes.

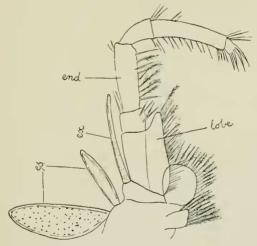
TEXT-FIG. 18.

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Koonunga the palp is still more developed, and the lower biting blade is reduced, being tipped with only three setæ.

The second maxilla (text-figs. 15, 16, 17) has a very uniform structure in the three genera. It may be interpreted as consisting of four gnathobasic lobes, a palp which has taken on the function of a gnathobase, and an exopoditic lobe, which is well developed in Paranaspides, much reduced in Anaspides, and absent in Koonunga.

The structure of this maxilla resembles that of the Mysi-



Text-fig. 19.

Paranaspides lacustris. First thoracic limb.

dacea more closely than that of the Euphausiacea, especially in the distinctness and arrangement of the gnathobases.

Among the fossil forms the structure of the mandibles and maxillæ has not been elucidated.

The first thoracic limb (text-figs. 18, 19, 20) differs only in detail from those of the following segments. It consists of a pediform endopodite with a reduced lamelliform exopodite. In Anaspides and Paranaspides the limb is composed of eight distinct segments, a protopodite of two joints and an endopodite of six. The coxopodite in both forms

bears a pair of delicate leaf-like gills externally, while internally, i.e. towards the month, two gnathobasic lobes are developed. The limb is flexed between the fifth and sixth segments, so that there are three segments distal to the "kneejoint" and five proximal to it. The terminal segment is short, and carries, as in all the thoracic limbs of the Anaspidacea, three enlarged setæ, of which the central one is the largest.

In Paranaspides the first joint of the endopodite (i. e.

Text-fig. 20.



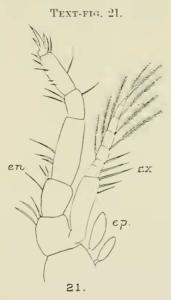
Koonunga cursor. First thoracic limb.

propodite) is expanded towards the month to form a definite lobe.

In Koonunga the structure of this limb is aberrant. The coxopodite is entirely without gnathobases. There are only seven segments in the limb, and since there are three segments distal to the "knee-joint" it is clear that a segment has disappeared from below, i. e. proximal to, this joint. There is no doubt that what has happened is that the propodite or first joint of the endopodite has fused with the basi-

podite, a process which can be observed to occur in some of the posterior limbs of Anaspides. If this is so, it is clear that the exopodite no longer springs from the basipodite, as it normally should do, but from the fused basipodite and propodite.

The second to the sixth thoracic limbs may be treated together, as they only differ in unimportant details. As a

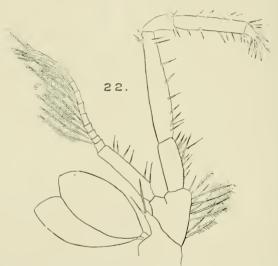


Koonunga cursor. Second thoracic limb. ex. Exopodite. en. Endopodite. ep. Gills.

type we may describe the fourth thoracic limb of Paranaspides (text-fig. 22). This limb is composed of a pediform endopodite and a flagellate exopodite borne on a two-jointed base. The coxopodite bears a pair of gills. We see in this limb the process of fusion of the basipodite with the propodite, the joint between them being represented by a groove which does not completely traverse the fused segments. In the more anterior limbs and especially in young specimens of both Anaspides and Paranaspides the groove may be complete. In the second thoracic limb of Koonunga (text-fig. 21), and indeed, in all the thoracic limbs of this form, the fusion of the basipodite and propodite is complete, so that the limb appears to be constantly formed of seven joints instead of eight. In all cases, nevertheless, there are constantly three segments above the "knee-joint."

In the female sex of all the three genera, the coxopodite of the fifth, sixth and seventh limbs bears on its internal

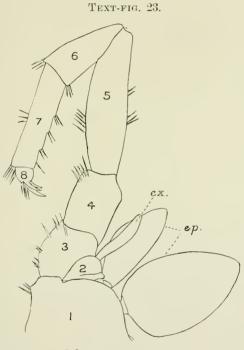
Text-fig. 22.



Paranaspides lacustris. Fourth thoracic limb.

face a small setose lobe (text-fig. 24). The function of this lobe, which is entirely confined to the female sex, is unknown, but since the lobes are only present in the hinder limbs in the neighbourhood of the oviducts and spermatheca, it may be suggested that they assist the process of fertilisation in some way. The openings of the oviducts in the female are situated on the coxopodites of the sixth pair of limbs (text-fig. 27).

The seventh thoracic limb differs from the foregoing in that in Anaspides and Paranaspides the exopodites are reduced to small unsegmented lamellæ, while in Koonunga they are absent altogether. In Anaspides the limb is eightjointed; the basipodite, carrying the exopodite, is very small, but separated from the propodite by a distinct groove. In Paranaspides this groove is very incomplete, while in Koonunga there is no groove at all, the two segments being



23. 🥌

Anaspides tasmaniæ. Seventh thoracic limb of male.

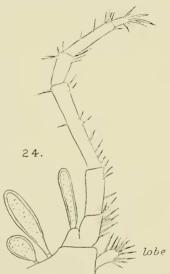
entirely fused. Attention has already been called to the presence of the setose lobe on the coxopodite of this and the two preceding limbs in the female sex.

The eighth thoracic limb (text-fig. 25) in all three living genera is composed of apparently seven joints, the second and third segments having no doubt, from the analogy of the preceding limbs, fused together. The exopodite has

completely disappeared and there are no gills attached to the limb.

In the male the openings of the vasa deferentia are situated on the inner edges of the coxopodites of the eighth thoracic appendage (text-fig. 26).

In the females of the three living genera a very conspicuous spermatheca is to be seen, placed between the last pair of thoracic limbs in the ventral middle line (text-fig. 27). It consists of a large conical papilla with a single median opening



Text-fig. 24.

Paranaspides lacustris. Seventh thoracic limb of female.

which leads into a wide tube. The tube bifurcates into two slightly ramifying passages in which spermatozoa may frequently be found. The tube and its passages are lined with chitin secreted by a definite epithelium, and round the ramifying bifurcations a cellular tissue is aggregated of a connective or supporting character, probably with much the same function as cartilage. This tissue is also found in the labrum, and its peculiar histological character is shown on Pl. 12, fig. 17.

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The presence of this spermatheca is of considerable taxonomic importance, as it appears to be entirely absent in the other Schizopods, viz. Mysidacea and Euphausiacea, but to

TEXT-FIG. 25.

25. Hill

Paranaspides lacustris. Eighth thoracic limb.

be present in certain of the more primitive Decapods. In the lobster and certain prawns a similar spermatheca is

TEXT-FIG. 26

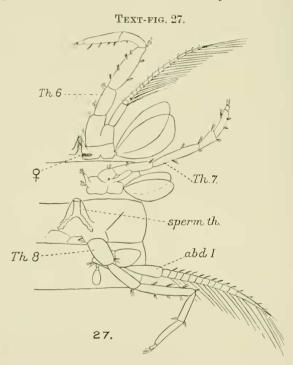


26.

Paran spides lacustris. Basal segment of eighth thoracic limbs, showing male openings.

present, and in the peculiar Eryonidea (Polycheles, Willemœsia) the presence of a spermatheca in the same position was pointed out to me by Mr. Gray, of the Oxford

University Museum. The investigation of this spermatheca in the female of Polycheles has revealed a structure identical with that of Anaspides. The spermatheca of Polycheles is a shield-shaped chitinous structure with a median opening leading into a tube which bifurcates exactly as in Anaspides.



Paranaspides lacustris,  $\mathcal{Q}$ . Ventral view of the last three thoracic appendages and first abdominal of left side in situ. *Th.* 6. Sixth thoracic limb. *Th.* 7. Seventh. *Th.* 8. Eighth. *Abd.*1. First abdominal. *Spermth.* Spermatheca.  $\mathcal{Q}$ . Female opening.

There can be no doubt that the structure in both cases is strictly homologons, and that we have in the spermatheca of Anaspidacea a Decapodan character, parallel to the presence of the otocyst on the first antennæ.

The thoracic limbs of the fossil Syncarida may now be dealt with as far as they are known, and those of Præanas-

pides (text-fig. 3), as being the best known, will receive first attention. The first thoracic limb is unknown. The second limb was apparently composed of three or four small basal joints and an expanded segment below the "knee," and probably three segments above the "knee." Except that no exopodite can be seen, it appears to have agreed with the corresponding limb of the living Anaspidacea. The succeeding thoracic limbs agree very perfectly with those of living forms. There was a two-jointed protopodite from which sprang a flagellate exopodite and a stout five-jointed endopodite, three of these segments being distal to the knee as in living Anaspidacea. In the last two thoracic limbs it is impossible to make out an exopodite, and this is again in agreement with the structure of the living genera. In the most perfectly preserved limbs it is only possible to make out seven segments in each limb, so that the fusion of the second and third segments may have already taken place in this form, but it is more probable that there were eight segments and that the condition of preservation does not permit us to see them all.

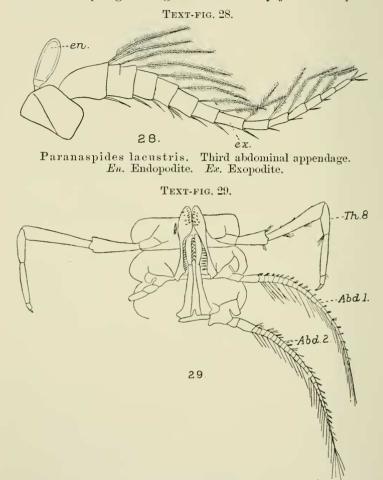
In Gampsonyx and Palæocaris we can only obtain a vague idea of the structure of the limbs. In the former the second limb was apparently of a raptorial nature, being greatly enlarged and furnished with prominent spines; the succeeding limbs one can only describe vaguely as biramous. In Palæocaris, if we can trust the diagrammatic reconstruction of Packard (text-fig. 56), the last six thoracic limbs were all similar and all biramous, with stont endopodites and slender exopodites.

In Gasocaris the endopodites are all similar and stoutly built, but Fritsch denies the presence of exopodites at all, a denial about which we may suspend our judgment, owing to the delicacy of the exopodites in the Anaspidacea and the difficulty of making them out even in the best preserved fossils.

The abdominal appendages, 1-5 in the females of Anaspides and Paranaspides, have all a very similar structure, except the fifth, which is without an endopodite. The

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limb consists of an expanded protopodite of two segments, from which springs a long setose and many-jointed exopodite

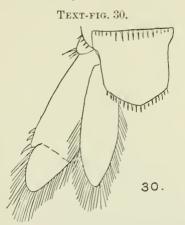


Paranaspides lacustris. First two abdominal appendages of male in ventral view in situ. Th. 8. Eighth thoracic limb. Abd. 1. First abdominal. Abd. 2. Second abdominal appendage.

and a very small flabellate endopodite. This endopodite is absent on all the first five abdominal appendages of Koonunga.

In the males the endopodites of the first two pairs of abdominal limbs are curiously modified as copulatory styles (text-fig. 29). They are large, hollow, club-shaped organs, well armed with setæ and hooks, disposed in a characteristic pattern, and the endopodites of the second segments fit into hollow spaces excavated in the first in a piston-like manner. The exopodites of these limbs are of a normal form.

The presence and structure of these copulatory styles is a distinctly Eucaridan feature, recalling similar structures in the Euphausiacea and Decapoda.



Anaspides tasmaniæ. Telson and uropods.

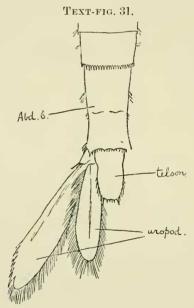
The abdominal limbs of Præanaspides show a long setose exopodite, much as in the living forms; the endopodite was apparently much reduced, as in living Anaspidacea. The reconstruction of Palæocaris also shows uniramons abdominal appendages, so that they also apparently agreed well with the living forms. The vague reconstruction of Gampsonyx shows us apparently biramous limbs with the two branches of equal length, but it is very likely that the long setæ on the exopodites have been confused with endopodites, an error that might occur in reconstructing Præanaspides.

The sixth abdominal limbs or uropods and the telson

have very characteristic forms, which are depicted in textfigs. 3, 30, 31, 32, 33, 55, 58, 61.

It will be noted that the uropods and telson of Paranaspides are more elongated than in the other genera, in correlation with the swimming mode of life.

Special attention must be called to the close correspondence between the uropods of Præanaspides (text-fig. 3) and Anaspides (text-fig. 30), even individual seta, e.g. those



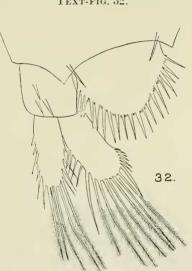
Paranaspides lacustris. Telson and uropods.

on the outer border of the exopodites, being practically identical in the two cases. The short setæ also upon the margin of the last two segments in Anaspides and Paranaspides are also represented in the fossil. The detailed correspondence in these and the other limbs of Anaspides, Paranaspides and Præauaspides permits us to place them with confidence in the same family. The uropods and telson of Gampsonyx, Palæocaris and Gasocaris agree on the whole very accurately with the

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other members of the Syncarida. The uropods and telson of Acanthotelson appear to have possessed a very aberrant form.

Attention may again be called to the observation of Professor Fritsch, that in Gasocaris and Gampsonyx an oval swelling is present near the base of the inner ramns of the uropod, which he interprets as an otocyst (text-figs. 55, 61). Nothing of the sort is to be observed in any of the living



TEXT-FIG. 32.

Koonunga cursor. Telson and uropods.

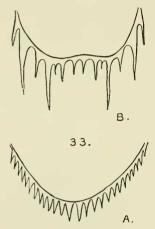
Anaspidacea nor in Præanaspides. If this structure really is an otocyst we are evidently dealing with a character which must have belonged originally to the Syncarida and the primitive Eumalacostraca, and has been retained in certain Peracarida (Mysidacea) but lost in the higher Syncarida, Peracarida and Eucarida.

(D) Theoretical Considerations.

A theoretical consideration of the appendages of the Syncarida with their associated organs will bring out several

points of importance. The nature of these structures is plainly of a generalised and primitive character. In the first place all the appendages, with the exception of the first antenna, are either typically biramous or have departed very little from the biramous plan. In the next place it is impossible, on the character of the appendages, to place the Anaspidacea in either the Peracarida or Eucarida, or any other division of the Malacostraca. The mandible is of a Peracaridan

TEXT-FIG. 33.



End of telson. A. In Anaspides tasmaniæ. B. Paranaspides lacustris.

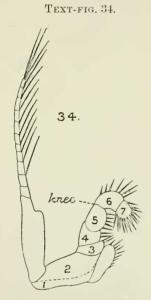
type, but lacks the lacinia mobilis; the maxillæ are possibly nearer those of the Peracarida than of the other divisions, but a palp is still present on the first maxilla and the exopodite of the second maxilla is greatly reduced.

On the other hand the otocyst on the first antennæ is paralleled only by the Decapoda, as is also the spermatheca at the base of the last thoracic limbs, while the copulatory styles are also Eucaridan.

The segmentation of the thoracic limbs is also very interesting as affording us a primitive condition from which that of the Peracarida on the one hand and that of the Eucarida on the other can be severally derived. We have seen that

the primitive Anaspidacean condition of these limbs is the possession of eight segments or joints, of which three are placed distally to the "knee" while five are placed proximally (e.g. text-fig. 18).

In the Peracarida and Eucarida we observe typically seven segments, but the "knee" in the two divisions, as pointed out by Hansen (14), is in a different position. In the Peracarida (e.g. Mysidacea) (text-fig. 34) there are two

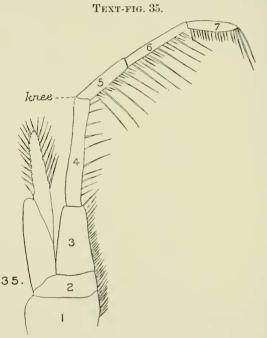


First thoracic appendage (maxillipede) of Macromysis flexuosa.

segments distal to the "knee," and primitively five proximal to it; in the Eucarida there are three segments distal to the "knee" and four proximal to it (text-fig. 35). Now we have seen that in the Anaspidacea there is a tendency for the second and third segments to fuse, and this process carried to completion would give us the Eucaridan limb. In the Peracaridan limb we may suppose that a segment has disappeared distal to the knee, probably the terminal segment, which in the Anaspidacea is very small.

In this manner it would appear that the "knee-joint" in Peracarida and Eucarida is homologous, while a different segment has been suppressed in each case, in the Peracarida the terminal segment, and in the Eucarida the second segment from the body, which has fused with the third.

Hansen has suggested that the claw usually present on the terminal joint of the Peracaridan limb represents the lost

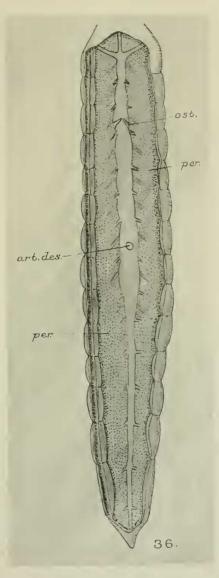


First thoracic appendage of Nyctiphanes.

terminal segment, and this may possibly be the case, though a theoretical refinement of this nature must always remain doubtful.

However this may be, the Anaspidacean limb with its eight segments gives us the generalised condition from which the Peracaridan and Encaridan types can be easily deduced.

Text-fig. 36.



Anaspides tasmaniæ. Dissection from dorsal surface, to show heart and pericardium (*per.*). Ost. Ostium. Art. des. Place of origin of descending or sternal artery from the heart.

- 3. INTERNAL ANATOMY (Anaspides tasmaniæ).
- (A) Pericardium, Heart and Vascular System.

If a median dorsal incision be made in An aspides, and the skin and dorsal muscles be turned away on each side, we find that we are in a spacious division of the body cavity with a very definite pigmented floor, which stretches from the first to the last segment. This space is the pericardium and its floor is pierced laterally in each segment by lacunar spaces which lead down into the cavities surrounding the bases of the appendages. The heart, which lies in the pericardium, is a long contractile tubular structure with an anterior expanded portion stretching from the first to the eighth thoracic segment; in the first abdominal segment it narrows considerably and is continued into a vessel which appears to be contractile, but is perhaps more rightly to be considered as a posterior dorsal aorta. The heart and aorta are fixed to the floor of the pericardium by a series of intersegmental short muscles, while the heart in the thoracic region is also supplied with segmental dorsal alary muscles. The heart is constricted intersegmentally where the ventral muscles attach it to the floor of the pericardium, but ostia are only present in one place, namely at the base of the third thoracic segment, where there appears to be a single pair.

Anteriorly the heart gives off three arteries, a median ophthalmic artery and paired antennary arteries.

In the seventh thoracic segment a sternal artery leaves the heart, and running obliquely downwards enters a ventral artery in the sixth thoracic segment, which runs forwards and backwards just dorsal to the nerve cord (text-fig. 44, *art. vent.*). A small subneural vessel is also present.

The elongated tubular heart is of a strictly Peracaridan type, and recalls very strongly the heart of the Mysidæ; the arterial system is of a generalised Malacostracan nature. The dorsal muscles which form the roof of the pericardium

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are arranged in four lateral longitudinal bands constricted intersegmentally.

The blood-corpuscles appear in sections as oval cells of varying size, but generally with similar nuclei. Above and to the sides of the cardiac division of the stomach there is a conspicuous mass of tissue with crowded darkly staining nuclei and without definite cell outlines, in which very numerous mitoses may be observed, even in an adult fullygrown animal. At the edges of this tissue, which lies free in the hæmocæl, cells can be seen to be detaching themselves which have the appearance of blood-corpuscles. This tissue (Pl. 12, fig. 2) is present in the same position in "Schizopoda" and Decapoda which I have examined, and there appears to be little doubt that it constitutes the blood-forming organ of the higher Crustacea in which the blood-corpuscles are reproduced.

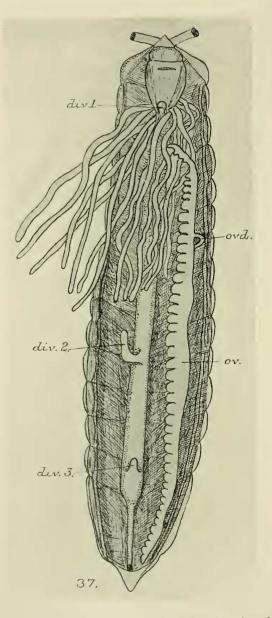
## (B) The Alimentary Canal.

On removing the heart and the floor of the pericardium we find the alimentary canal with its associated glands. We will first shortly enumerate the various parts of the alimentary canal, beginning from in front backwards.

The short dorso-ventrally directed œsophagus leads into an expanded stomach which is furnished with a series of complicated setose ridges. At the pyloric end of the stomach a short median dorsal diverticulum marks the position where the mid-gut or endodermal portion of the alimentary canal begins and the stomodæum ends. At the same point, but ventrolaterally, a great number of long, slender, liver cæca enter the stomach, to the number of about thirty.

The mid-gut is continued downwards as a straight tube until the second abdominal segment, where a large and conspicuous dorsal diverticulum is given off. This diverticulum, which is of a glandular nature, belongs to the mid-gut, but it does not mark the place where the proctodæum begins. This position is marked by a third diverticulum in the fifth abdo-

Text-fig. 37.

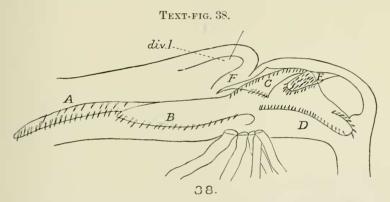


An aspides tasmaniæ. Dissection from dorsal surface, heart and pericardium removed, to show ovary (ov.) on one side and alimentary canal. Left ovary removed. Ovd. Oviduct. Div. 1. First dorsal diverticulum. Div. 2. Second. Div. 3 Third.

minal segment, which also belongs to the mid-gut, but immediately below it the character of the epithelium entirely changes, and a chitinous lining, marking the proctodæal invagination, covers the internal surface of the intestine. The anus opens ventrally on the telson.

We will now describe these various portions in more detail.

The stomach may be divided into an anterior cardiac and a posterior pyloric portion. The division between them is marked dorsally by the first diverticulum of the alimentary



Anaspides tasmaniæ. Stomach removed from body and viewed laterally. For lettering see text.

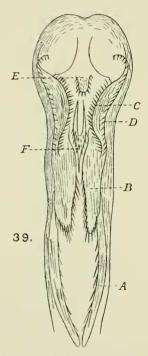
canal, and ventrally by the entrance of the liver cæca, so that the cardiac portion is stomodæum while the pyloric is endodermal, although chitinous pieces of ectodermal origin are projected into the pyloric division.

The cardiac portion of the stomach is furnished with a pair of lateral elevations carrying setæ. Each lateral elevation is in the form of an incomplete circle, the setæ being present in two main pieces of the ridge, viz. c and D in text-figs. 38, 39, 40. There is also present a median setose prominence (E), and a more posteriorly placed tooth (F) which projects into the pyloric cavity. In the median ventral line there is a prominent pad (H) (text-fig. 40) which projects

into the cavity of the stomach and stretches into the pyloric portion (see also transverse section, Pl. 12, fig. 3).

The pyloric portion of the stomach is furnished with a pair of very long setose ridges on each side, the hindermost ridge of each side being produced backwards far down the intestine (A and B, text-figs. 38, 39, 40).

Text-f1G. 39.



Stomach from dorsal surface, showing chitinous ridges, etc.

In comparing this armature of the stomach of Anaspides with other Malacostraca, I make use especially of Gelderd's useful work on the digestive system of the Schizopoda (15).

The lateral pieces of the cardiac division (C, D) correspond to Gelderd's ridges s, which he finds to be present in all Malacostraca; similarly the lateral pieces of the pyloric division (A, B) correspond to his ridges  $s_2$ , which are also

universally present. The median pieces (E and F) correspond to the urocardiac ossicle and median tooth of the Decapoda. The piece (E) is present in most Malacostraca, but the posterior piece (F) possibly points to Decapodan affinities. The great length of the lateral pyloric pieces (A and B) in Anaspides resembles the condition of the Euphausiidæ and not that of the



Stomach from ventral surface.

Peracarida, in which these pieces are short. Again, in the Peracarida there is a complicated median ventral ridge in the pyloric division, which in the Euphansiidæ is simpler and appears to be absent in the Anaspides, while the elongated ventral ridge (H) in the cardiac division of Anaspides recalls closely that of the Euphausiidæ. We may therefore conclude that in those points in which the gastric mill is not merely Malacostracau, it inclines to the Eucaridan rather than the Peracaridan type.

The first dorsal diverticulum to the gut is a thickwalled pocket which opens into the pyloric division of the stomach by two lateral passages on the outside of the lateral pyloric ridge (B). In the section shown in Pl. 12, fig. 4, only one lateral opening is seen on the right side.

The histological character of this diverticulum is extremely puzzling (Pl. 12, fig. 4). It consists of thick walls in which crowds of nuclei are densely packed without definite celloutlines round them, and many of the nuclei are seen to be either actually undergoing mitosis or else in preparation for division. This process of mitotic division is to be observed in fully grown adult specimens, so that we are evidently dealing with a tissue which remains in a permanently embryonic condition. There are no cells of a glaudular nature in this diverticulum, as might well be expected from its position on the alimentary canal.

It is impossible to do more than guess at the function of this remarkable organ, but from the active reproduction of the cells composing it, it may be suggested that its function is to supply new epithelial cells for the lining of the alimentary canal as the old cells wear out and become effete.

Laterally the walls of the first diverticulum pass into the epithelium of the mid-gut or endoderm (Pl. 12, fig. 5). The portion of the mid-gut lying between the first and second diverticula is essentially glandular in nature, especially in the anterior and dorsal region. In this region the epithelial cells are tall and columnar. The majority of these cells have lightly-staining oval nuclei, but wedged in between these ordinary columnar cells are nests of much-flattened cells with spindle-shaped nuclei, which stain intensely with hæmatoxylin. These cells are apparently special gland-cells of some kind, which pour a secretion into the gut. Ventrally and posteriorly the lining epithelium of the mid-gut is composed of short cubical cells with rather darkly staining nuclei.

The basement membrane of the mid-gut is remarkably

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thick and conspicuous; and it is thrown into marked sinuosities of outline; this membrane stops abruptly when the mid-gut passes over into stomo- or proctodæum. Exteriorly to the basement membrane is a thin submucous layer with flattened darkly-staining nuclei (Pl. 12, fig. 5).

The second dorsal diverticulum of the mid-gut is by far the largest. Histologically (Pl. 12, fig. 6) it is simply formed as a pocket from the dorsal mid-gut epithelium, and its cells are elongated and columnar with very numerous nests of flattened special gland-cells. There can be no doubt about the function of this diverticulum; it is simply a digestive gland which pours its secretions into the alimentary canal.

The remaining portion of the mid-gut lying between the second and third diverticula is of a simple structure, and is evidently chiefly of an absorptive nature (Pl. 12, fig. 7). The epithelium is composed of short columnar cells with striated outer borders; the basement membrane, characteristic of the mid-gut, is still to be observed, while the submucosa forms a thick reticular layer in which large homogeneously staining nuclei are embedded. There are no gland-cells in this region.

The third dorsal diverticulum is exceedingly small, and is composed of columnar cells and numerous nuclei embedded in a common protoplasm. There are no special gland-cells. A fair number of mitoses can always be observed in this diverticulum, though not so many as in the first diverticulum; its function may be similar to that suggested for the first, viz. to keep up a supply of epithelial cells for the lining of the alimentary canal. The intestine behind the third diverticulum is proctodænm, being lined internally with chitin, which is thrown into numerous folds. The epithelium is columnar and hyaline, being very similar to that of the stomodæum.

It remains to describe the liver. This organ is composed of very numerous slender tubes, as many as thirty being often present, which open ventrally into the pyloric division

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of the stomach by a wide common opening. The histological character of these tubes varies greatly according to the condition of metabolism. A transverse section through the middle of a tube, when the animal is starved, shows a regular lining of tall columnar cells, the majority of which have hyaline, reticular cytoplasm, staining pink with eosin, and granular nuclei (Pl. 12, fig. 8). These cells are mainly absorptive in function. Scattered among these cells are narrower cells with rather coarsely granular cytoplasm, which is darkly coloured with hæmatoxylin. These cells are special gland-cells and probably secrete a ferment.

At the ends of the tubes the nuclei are greatly crowded, but both kinds of cells can be recognised.

After feeding heavily, the histology of the tubes changes (Pl. 12, fig. 9). The special gland-cells are no longer recognisable, and the absorptive cells lose their definite cell-outlines and are distended with oily globules. Certain of the cells consist merely of an envelope containing an immense vacuole with a darkly staining nucleus flattened on one side. The liver of Anaspides therefore has, at least, two distinct functions; it produces digestive ferments which are poured into the stomach, and it also plays an important part in the absorption and storing of assimilated material.

If we compare the alimentary tract of Anaspides with that of other Malacostraca we see that the structure of the stomach points rather to Eucaridan affinities. The presence of dorsal diverticula at the juncture of endodermal mid-gut with stomodæum and proctodæum is a Decapodan character, since in the "Schizopoda," i.e. Euphansiidæ and Mysidæ, etc., there is never a diverticulum between mid-gut and proctodæum. We have seen that there is also another diverticulum in the middle of the mid-gut, and this character is, as far as we know, peculiar to Anaspides and its immediate allies.

The liver, although in certain respects peculiar, is nearer to the Eucaridan plan than to the Peracaridan, since in the latter there is typically present a glandular ridge upon which the

gland-cells are concentrated, while in the Eucarida and Anaspides the gland-cells are distributed about among the absorptive cells.

On the whole, therefore, the alimentary tract of Anaspides, while showing certain peculiar features, points to Encaridan and especially Decapodan affinities.

# (c) Excretory System.

The excretory organ of Anaspides is situated at the base of the second maxilla; it is a maxillary gland. We can distinguish four chief regions: (1) A straight excretory duct with rather thick walls and darkly staining somewhat flattened nuclei (Pl. 12, fig. 10). This duct passes into the base of the second maxilla on each side and opens by a pore on the external border of the appendage. (2) The excretory duct passes internally into a coiled excretory tube with striated walls and greatly flattened darkly staining nuclei (Pl. 12, fig. 11). (3) This coiled tube passes insensibly into another coiled tube with an epithelium of a more glandular nature and with oval nuclei containing granules of chromatin (Pl. 12, fig. 12). The cytoplasm of these cells is more granular but has a faintly striated appearance. (4) The glandular tube is coiled into an expanded sac, the end-sac into which it opens. The end-sac is lined with a flattened epithelium, the cells of which contain globules of a vellowish colour (Pl. 12, fig. 13).

The presence of a maxillary gland, and the entire absence of an antennary gland, is only found elsewhere in the Malacostraca among certain Isopods and in Nebalia. It is unknown either in the "Schizopoda" or Decapoda.

# (D) Reproductive Organs.

Female.—The external sexual characters of the female, together with the spermatheca, have been described (pp. 516-518). The ovary of an adult Anaspides is a lobed

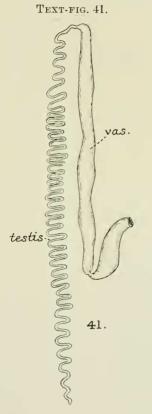
structure stretching from about the second thoracic segment to the extreme hind end of the abdomen (text-fig. 37). If we take a horizontal section through the ovary (Pl. 12, fig. 14) we see that the lobes contain small immature ova while the external part of the tube is filled with large, nearly mature ova filled with a purplish yolk. The external wall of the lobed portion consists of small undifferentiated cells of the germinal epithelium. The inner wall of the ovary consists of cells, most of which contain large nuclei which stain of an uniform dark colour with hæmatoxylin, while there is present a number of granules which stain deep black. These cells may be called the trophic cells. On their inner borders they are vacuolated, and it is evidently their function to elaborate food material, which they supply in the form of yolk to the developing ova. A certain number of these trophic cells can be seen lying among the eggs in the middle of the tube. The oviducts are simple straight tubes lined with short columnar cells; they pass below the ventral muscles to open on the coxopodites of the sixth thoracic limbs. They are not supplied with any accessory glands.

Male.—The testes (text-fig. 41) are coiled tubes running from the anterior thoracic region to the extreme hind end of the body. At the anterior end of the coiled tube a duct passes posteriorly, and then turning anteriorly again opens at the bases of the eighth thoracic limbs.

In the glandular part of the testis of a young Anaspides we can study the process of spermatogenesis (Pl. 12, fig. 15). We see the primary and secondary spermatocytes undergoing mitosis, and fully-formed spermatozoa. On the outside of the tube we see large cells with darkly staining nuclei of an exactly similar appearance to the trophic cells found in the ovaries. These cells are not, however, to be observed in an adult testis. In an adult testis we only see nests of spermatocytes in various stages of spermatogenesis, or else groups of fully formed spermatozoa.

The upper part of the descending duct is sterile, so far as the production of spermatozoa is concerned, and it is formed

purely of trophic cells (Pl. 12, fig. 16). The lower portion of the duct has a thick epithelial wall with oval granular nuclei, and these cells produce an albuminous material that is cast into the lumen of the duct and solidifies round the



Anaspides tasmaniæ. Testis and vas deferens of one side.

spermatozoa to form the spermatophores. There is a thick muscular layer surrounding the lower part of the vas deferens. In the section (Pl. 12, fig. 16) the top of the spermatophor, with its albuminous coat, is cut across.

The spermatozoa are filiform elongated bodies with a con-

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spicuous globular head and a long flagellum (text-fig. 42). They resemble closely the spermatozoa of all the Peracarida.

The spermatophores are horseshoe-shaped bodies about half an inch in length, with a constriction near the middle. They possess a fine chitinous investment on the outside, as well as



Spermatozoon of Anaspides tasmaniæ. × about 50.

the albuminous material within. They are placed by the male into the spermatheca of the female, where they may be sometimes found protruding their horn-like ends to the

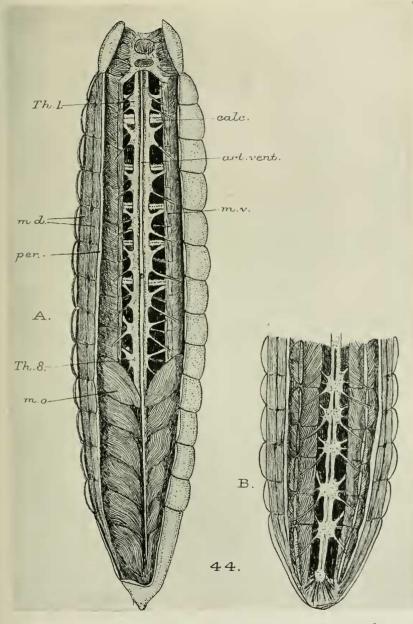
TEXT-FIG. 43.



Spermatophores of Anaspides tasmaniae.  $\times$  3.

exterior. After the spermatozoa have passed out of them into the spermatheea they soon drop off.

The filiform character of the spermatozoa is a Peracaridan character; the presence of definite spermatophores is Eucaridan.



Anaspides tasmaniæ. Alimentary canal and gonads removed to expose nervous and muscular system. A. With abdominal oblique muscles (m.o.) in situ. Th. 1. First thoracic ganglion. Th. 8. Eighth thoracic ganglion. calc. Calcareous band between ganglia. art. vent. Ventral artery. m.v. Ventral muscles. m.d. Dorsal muscles, cut through and turned back. per. Edge of pericardium, which has been removed. B. After removal of oblique muscles to show six abdominal ganglia.

## (E) Muscular System.

The dorsal muscles which lie above the pericardial space form four dorso-lateral, segmented, longitudinal bands running the entire length of the body. The oblique muscles are segmented bundles running obliquely downwards in each segment; they are very much larger in the abdominal segments than in the thoracic. Segmentally arranged ventral bands are also present, which again are larger in the abdominal than in the thoracic region. In order to see them and the nerve-cord in the abdomen, the oblique muscles have to be removed.

### (F) Nervous System.

We will deal first with the nerve-cord behind the subcesophageal ganglion. There are in the thoracic region eight distinct ganglionic thickenings, one for each free thoracic segment: similarly in the abdomen there are six ganglia (text-fig. 44).

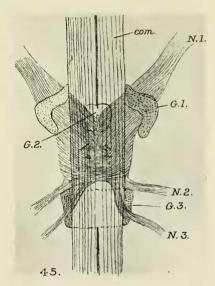
There are five bands of calcareous concretions situated between the first six thoracic ganglia (*calc.* text-fig. 44). This is the only place where lime is present in the whole of the body.

Each thoracic ganglion gives off three chief pairs of nerves: an anterior thick pair which pass forwards to the appendages of the segment; a more posterior slender pair which appear to supply the ventral muscles of each segment; and a still more posterior pair which innervate the oblique muscles. If we examine a single thoracic ganglion more carefully by means of sections, we may obtain a diagrammatic reconstruction, such as is shown in text-fig. 45. The inter-ganglionic commissures (com.) are seen to fuse above and below the ganglionic area, but their fibres are continuous right through that area on the dorsal surface. The large nerves (N, 1) to the appendages send their fibres ventral to the commissural

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fibres, and in the gauglion they form thick bundles of transverse commissures which anastomose in the thick fibrous region in the ventral middle line. A gauglionic mass is applied to the dorsal surface of this nerve (G.1) and also to the ventral (G.2). The two nerves to the muscles are seen issning more posteriorly from the gauglion; their fibres also lie ventral to the commissural longitudinal fibres. A



TEXT-FIG. 45.

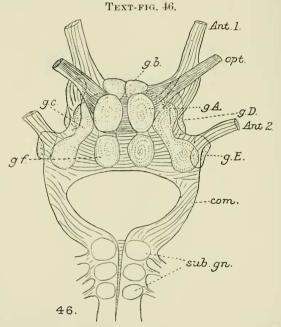
Reconstruction of a thoracic ganglion of Anaspides tasmaniæ. com. Longitudinal commissures of cord. N. 1. Nerve to appendage. N. 2. Nerve to ventral muscles. N. 3. Nerve to oblique muscles. G. 1. Dorsal ganglionic mass. G. 2 and 3. Ventral ganglionic masses.

ganglionic mass (G, 3) is situated only on the ventral surface at the exit of these nerves.

The brain or supra-cesophageal ganglion gives issue to three nerves, the optic (opt.), antennulary (Ant. 1), and antennary (Ant. 2) nerves.

The optic nerves spring from the dorsal surface of the brain, being the only nerves with this position of origin.

Where they enter the brain there is a dorsal ganglionic mass (text-fig. 46, g. A.). The dorsal ganglionic masses (g. C.) belonging to the antennary nerves are applied anteriorly to the ventral root of the optic nerve, and it is possible that this part of the ganglionic mass (g. C.) really belongs to the optic nerve. If this were so, the optic nerve would be supplied with a dorsal



Reconstruction of brain of Anaspides tasmaniæ. Ant. 1. Antennulary nerve. Ant. 2. Antennary nerve. Opt. Optic nerve. g.A. Dorsal ganglionic mass applied to root of optic nerve. g.F. Its posterior continuation. g.B. Ganglion applied to root of Ant. 1. g.C. Ganglion applied dorsally to root of Ant. 2. g.D. Ganglion applied ventrally to root of Ant. 1. g.E. Ganglion applied ventrally to root of Ant. 2. Com. Pericesophageal commissures. sub. gn. Subcesophageal ganglion.

and ventral ganglionic mass, as in the case of a regular trunk nerve. Lying dorsally in the brain there is a bundle of transverse commissural fibres forming a regular optic chiasma.

The antennulary nerves (Ant. 1) enter the brain ventrally

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and are supplied with a dorsal (G. B.) and ventral (G. D.)ganglionic mass on each side. Their fibres form thick transverse longitudinal bands in the ventral part of the brain, with complicated branches passing posteriorly. The antennary nerves (Ant. 2) enter the brain laterally and ventrally, and are supplied with a very large dorsal ganglionic mass (G. c.), which passes anteriorly underneath the fibres of the optic nerves, and a smaller ventral mass (G. E.). The fibres which enter the brain from these nerves form a very complicated and massive system, occupying the whole of the posterior part of the brain.

The peri- $\infty$  sophageal commissures (com.) are short, and ventrally to the  $\infty$  sophagus they come together in the sub- $\infty$  sophageal ganglion (sub. gn.), which gives off three nerves to the mandible and two pairs of maxillæ.

# (G) Theoretical Considerations.

If we pick out the more important points in the internal anatomy of Anaspides, in order to compare it with the other Malacostraca, we perceive that its internal anatomy is of a generalised type resembling in some respects the Peracarida and in others the Eucarida, especially the Decapoda.

The chief Peracaridan features are the elongated, tubular heart and the filiform spermatozoa, while the possession of a maxillary gland is paralleled by certain Peracarida (Isopoda). The alimentary canal, on the other hand, in so far as it is not peculiar, recalls that of the Decapoda. The nervous system is of an unconcentrated primitive character, with a discrete ganglion in each thoracic and abdominal segment.

Comparing these conclusions with those derived from a consideration of the external characters, we may observe that they are in complete agreement. From the external characters of the limbs and of the segmentation we judged that the Anaspidacea stood midway between the Peracarida and the Eucarida, but on a more generalised and primitive plane,

from which either of the two divisions might be derived. We also saw that the Anaspidacea, in their external characters, approached nearer to the Decapoda, than to the Euphausiid type of the Eucarida, and this, again, appears to be the case in the internal anatomy. This would indicate that the Euphausiacea are a late offshoot from the Decapodan stock, and if this conclusion is accepted it is evident that the old group of the Schizopoda, including the Mysidacea, Euphausiacea and Anaspidacea is an unnatural assemblage and must be abandoned (see phylogenetic tree on p. 551).

4. BIONOMICS : (HABITS, REPRODUCTION AND DISTRIBUTION).

(A) Habitat and General Habits.

An aspides tasmaniæ inhabits deep pools of rivers or tarns on the mountains of southern and western Tasmania; the water in which it lives is always absolutely clear and cold, and the animal clambers about upon the stones or among the submerged mosses and liverworts at the bottom of the pools. It very rarely swims, though it occasionally does so in a lazy fashion, and it will occasionally rise to the surface of the water and turn over on to its back in the manner of a Phyllopod. Its usual mode of progression is walking or running in the attitude presented in Pl. 11, fig. 1; when alarmed it darts forwards or sideways by powerful strokes of its abdomen and tail-fan. I never observed it to spring backwards, a movement of which it appears to be incapable.

The exopodites of the thoracic limbs are not used in locomotion to any appreciable extent, their function being to keep the water agitated round the gills and so assist in respiration. Even when the animal itself is stationary the exopodites can be seen to be in a continual waving motion.

As remarked before, the body is always held perfectly flat and unflexed whether the animal is walking, swimming, or at rest.

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They appear to be omnivorous, as they will feed upon the dead bodies of insect larvæ or even upon one another, but their chief food is the algal slime covering the rocks among which they live, and they also browse upon the submerged shoots of mosses and liverworts.

The rivers and tarns in which they live are singularly free from any enemies such as predaceous fish which might prey upon them, the only fish inhabiting these highland waters being the little "Mountain Trout," Galaxias truttacens. The English Trout, which have multiplied so wonderfully in the Tasmanian streams and lakes, have hardly penetrated to the mountain fastnesses where Anaspides dwells.

The only parasite found infecting Anaspides is a peculiar species of neogamous gregarine which lives in the free state in the alimentary canal and forms large associated cysts in the liver-tubes, often in very great numbers. This gregarine will shortly be described in this journal by Mr. J. S. Huxley.

Paranaspides lacustris is known only from the specimens collected by me in the great Lake of Tasmania at an elevation of 3700 ft., where it inhabits the littoral region, living among the weeds and stones at a small depth rather after the manner of a prawn.

Its markedly humped back and translucent green colour give it very much the appearance of a small prawn, e.g. Hippolyte, and it follows more of a swimming habit than Anaspides, but in other respects it resembles the latter closely. It doubtless falls an easy prey to the great quantities of large English brown trout which inhabit the lake, and it is probably in danger of an early extinction.

Koonunga cursor has been found hitherto only in a small runnel issuing from the Mullum Mullum Creek, Ringwood, to the west of Melbourne, and it is the only member of the living Anaspidacea which lives at a low level. In general appearance and habits it resembles Anaspides more closely than Paranaspides does, although it is morphologically very distinct. The specimens which Mr. Sayce

kindly showed to me ran about with great activity, keeping the body perfectly flat and unflexed as in Anaspides.

# (B) Distribution.

We have seen that the living Anaspidacea are all confined to the temperate part of the Australian region, called by Professor Spenser the Bassian Subregion, where they inhabit exclusively fresh water, usually at a high elevation, where at any rate the winters are exceedingly cold. The fossil Anaspidacea, on the other hand, are, as far as we know, confined to the marine deposits of the northern hemisphere, being found in the Permian and Carboniferous deposits of Europe and North America. I have suggested elsewhere (12) that animals with this type of distribution, viz. in the north temperate hemisphere and in the Alpine regions of temperate Australia, probably have reached their present position in the southern hemisphere through South America and the submerged Antarctic Continent, and not through the tropics of Asia and Australia. Although this is little more than a tentative suggestion, it is, perhaps, justifiable to predict that living members of the Anaspidacea may still be found in the temperate fresh waters of South America or New Zealand.

# (c) Breeding and Reproduction.

The breeding of A. tasmaniae appears to go on through the early summer months (December to April) as the pools on Mt. Wellington were continually being replenished with young of a very small size. Since there is no brood-pouch, it was of interest to establish what the female does with her eggs, especially as this is a character of great taxonomic importance. By keeping the animals in captivity it was observed that the male deposits two very large spermatophores in the spermatheca of the female. These spermatophores are large curved structures with a thin chitinons coat (text-fig. 43), and they project outside the sperma-

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theca. The spermatozoa pass into the spermatheca and the spermatophores drop off. Fertilisation appears to take place in the oviducts, since in some sections of Koonunga shown to me by Mr. Sayce, spermatozoa could be seen lying in the basal part of the oviducts. As to how the spermatozoa reach the oviducal openings from the spermatheca there is some doubt, but it seems probable that they are assisted in this migration by the peculiar setose lobes on the internal faces of the last three pairs of thoracic appendages, which are only present in the female.

The female deposits and hides the fertilised eggs, which are of a purple colour and measure about 2 mm. in diameter, singly and not agglutinated together, under stones and among the roots of water plants (Pl. 12, fig. 3). This peculiar habit of oviposition is only found elsewhere among the Malacostraca in certain forms of Euphausiidæ which may have pelagic eggs; in all other Malacostraca they are either carried in a brood-pouch (Phyllocarida and Peracarida), or else glued on to the abdominal limbs (Eucarida), or carried in a special chamber formed by the maxillipedes (Hiplocarida). Among Entomostraca the only forms which deposit their eggs are the Argulidæ.

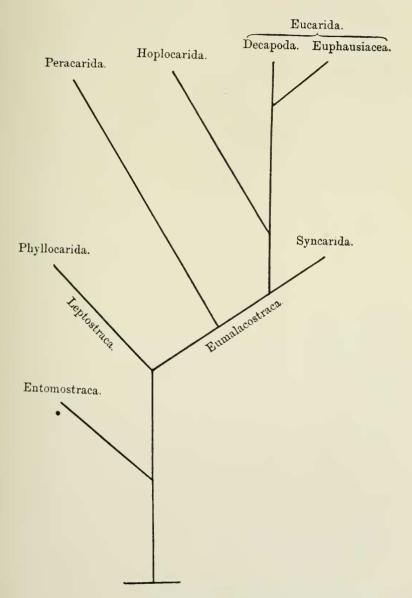
As to the development of the eggs or the presence of any larval stages my observations are unfortunately very few. I am, however, convinced that no complicated metamorphosis is passed through, as the pools under my observation were continually being replenished by minute Anaspides of 4-5 mm in length, which already possessed the complete adult structure. It is also quite impossible that pelagic larvæ of such types as the Nauplius and Zoæa could be assumed, as they would at once be swept away in the mountain torrents down to the lowlands, where Anaspides, as a matter of fact, never occurs. It is possible, however, that the young are hatched out from the egg, not with the complete adult structure, for Mr. Sayce (10) found a minute specimen of Koonunga in which the abdominal appendages were incompletely developed.

5. THE RELATION OF THE SYNCARIDA TO OTHER MALACOSTRACA.

The examination which has been made in the foregoing pages of the chief characteristics of the Syncarida has convinced us that they are the most generalised group of the Eumalacostraca. We have also seen that the structure of the living representatives of the division is practically identical with that of fossils which date, at any rate, from the Carboniferous period, so that they are among the oldest Malacostraca, with the exception of the Nebaliacea, known. Their generalised and primitive nature is not only shown by their great antiquity and by the possession of such characters as the freedom of all the thoracic somites, and the presence of eight joints in the thoracic limbs, but also by the fact of their combining in their own structure many of the distinctive characters of the two divergent groups of the modern Eumalacostraca, viz. the Peracarida and the Eucarida. Thus we have seen that they possess the anditory organ, the alimentary canal and its glands, the spermatheca and copulatory organs of the Eucarida, but at the same time the structure of the heart and of the spermatozoa, the absence of a carapace, the direct mode of development and the maxillary gland point to Peracaridan affinities.

The Syncarida, therefore, represent to a great extent the ancestral form from which the Peracarida and the Encarida have diverged. It has also been pointed out that the Syncarida are closer to the Decapoda than to the other order of the Encarida, viz. the Euphausiacea, so that the latter, so far from being the primitive Eucaridan type, must be considered as a specialised offshoot from the main Decapodan stem, which has lost certain primitive and ancestral characters. In fact, the only primitive character retained by the Euphansiacea is the biramous structure of the thoracic limbs, and this has also been retained by the lower members of the Decapoda, and so is not particularly significant.

In the following phylogenetic scheme we have given expression to this idea.



Phylogenetic Tree, showing chief lines of descent in the Crustacea. VOL. 53, PART 3.-NEW SERIES. 38

The position of the Hoplocarida (Squillidæ) as an early offshoot from the Decapodan stem must remain at present doubtful, but many of their characters point to this conclusion. The spherical spermatozoa, the ramified hepatic cæca, the complicated metamorphosis, the absence of a lacinia mobilis, the presence of an appendix interna on the pleopods, all suggest that the Hoplocarida have travelled some way in the Eucaridan direction since their derivation from the common Eumalacostracan ancestor. That this Eumalacostracan ancestor which diverged from the Leptostracan stock was not identical with the Syncarida must probably be conceded. But we may perhaps conceive of it as a straight-bodied ambulatory Crustacean without a carapace and with all the thoracic segments free and uncoalesced, with a tail-fan and with all its thoracic and abdominal appendages biramous. The thoracic limbs consisted of eight joints, three of these joints being distal to the "knee." It possessed stalked eves, an antennal scale, and two flagella on the antennules, and it possibly lacked an otocyst on the antennules. Internally the heart was elongated, the alimentary canal had, perhaps, only an anterior dorsal diverticulum, and the liver-tubes were few and simple. The spermatheca were filiform and there was present both an antennary and maxillary gland. It probably had a brood-ponch as in the Phyllocarida.

From this type it was but a step to the Syncarida. Directly from this ancestral type sprang the Peracarida, with their characteristic brood-pouch; a certain amount of fusion of segments either with the head or with one another took place, and certain of them developed, independently of the Eucarida, a carapace.

The Eucarida were probably derived from an ancestor which had travelled some way in the Syncaridan direction, that is to say, it had an otocyst on the antennules, it had lost the brood-pouch, and it had developed certain other characters, such as the spermatheca and copulatory styles and a more complicated liver and alimentary canal. As it diverged from the primitive Syncarida it acquired a carapace, spherical

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in place of filiform spermatozoa and a short triangular heart ; it specialised an antennary gland and it possessed a complicated metamorphosis. After its divergence it threw off the Hoplocarida and the Euphausiacea.

If this phylogenetic scheme for the Eumalacostraca be accepted it is clear that we can no longer look upon the old order "Schizopoda" as a natural assemblage standing at the base of the Eumalacostracan stock. This classification rests solely on the biramous structure of the thoracic limbs, and ignores all the other organs, whether external or internal, in which the various divisions differ so fundamentally.

We must remain in some doubt as to the presence or absence of certain characters in the ancestral Eumalacostracan which gave rise to the Syncarida, Eucarida and Peracarida. With regard to the brood-ponch it may well be that this has been independently acquired by the Leptostraca and the Peracarida, and that its absence in the Syncarida represents a primitive condition. Again, the otocyst on the antennules may have been possessed by the ancestral Eumalacostracan and lost by the Peracarida. In this connection we may mention the striking observation of Professor Fritsch, according to which an otocyst was present on the inner ramus of the uropods in the fossil Syncarida, Gasocaris and Gampsonyx. If an otocyst was really present in this position in these forms we can only suppose that the primitive Eumalacostracan possessed it, and that it has been retained by only a few Peracarida (Mysidacea), and entirely lost by the higher Syncarida and Peracarida and by the entire division of the Eucarida.

The reconstruction of the phylogeny of the Malacostraca, therefore, leads to the reflection that the primitive ancestors of the specialised groups are not distinguished from their modern representatives so much by simplicity of structure, but rather by combining in themselves the heterogeneous elements which have been segregated out in the course of evolution and separated into the different streams of descent that have given rise to the modern groups. It was the habit of morphologists, and perhaps still is, to imagine that a primitive ancestral form must have been simpler and have exhibited less complication of structure than its modern representatives. In pursuance of this preconceived notion the simplest organised members of a phylum or smaller group of animals was always hit upon as representing the ancestral form; but too often it has been shown that this simplicity is the result of secondary degeneration or simplification of structure. We have only to mention the Archianelida and the Marsupials to indicate what has been the trend of morphological opinion on this subject.

It is often complained, especially by naturalists immersed in the positive details of what may appear more modern and fruitful branches of inquiry, that speculative morphology, as a reputable department of biology, is dead, killed by the wild speculations of its devotees. But it may have escaped their attention that the tendency of speculative morphology to-day is to display a more cautious temper than heretofore, and instead of attempting to link phyla with phyla by golden bridges of aërial speculation to undertake the more modest task of tracing the lines of descent within a smaller range of organisms, the history of whose evolution has been accomplished at any rate somewhere within the period of time represented by the stratified rocks.

If the family Anaspididæ was already fully differentiated in the Carboniferous period and the family Nebaliidæ in the Cambrian, it may well be conceded that to look for the ancestor of the Crustacea or to prove that Peripatus really links the Arthropoda and Annelida together are tasks which the cautious morphologist may well abjure. But that speculative morphology, when content to deal with the phylogenetic history of fairly confined and homogeneous groups whose fossil ancestry have been preserved for us through a long period of time, is altogether idle we need not admit. And if a general consensus of opinion might at some future time be achieved, that the process of evolution in such groups has not been effected by the gradual complication of an originally simple structure and by the addition of new organs to comparatively undifferentiated organisms, but rather by the segregation and separation of characters originally combined in one ancestral form into the various streams of descent which have emerged from it—if this opinion might at any time be adopted and sustained, it would influence our attitude to the philosophy of evolution as profoundly as any conceptions deduced from the experimental study of living organisms, without reference to the history which they have passed through.

## 6. Systematic Part.

The Anaspidacea, living and fossil, are placed in a separate division of the Eumalacostraca. Thus:

## Division Syncarida (Packard 5 and 6, Calman 9).

A carapace is absent. The thoracic somites are either all distinct, or the anterior one may be fused to the head. The eves are pedunculated or sessile. An otocyst is present on the basal joint of the antennules. The antennal protopodite consists of two segments. The mandible is without a lacinia The thoracic limbs consist typically of eight segmobilis. ments, and the "knee-joint" is between the fifth and sixth segment. There are no oostegites. A spermatheca is present on the last thoracic segment of the female. There is no appendix interna on the pleopods. The endopodites of the first two pleopods of the male are modified to form copulatory styles. The branchiæ form a double series of leaf-like plates on all but the last or last two thoracic limbs. The heart is elongated and tubular. The alimentary canal is furnished with three dorsal diverticula, one at the junction of the stomodæum and mid-gut, one in the middle of the mid-gut, and one at the junction of the mid-gut and proctodæum. The hepatic cæca are numerous, elongated unbranched, and without glandular ridges. and The

excretory organ is a maxillary gland. The spermatozoa are filiform, and are transferred to the female in horn-shaped spermatophores. There is no concentration of ganglia in the thoracic or abdominal region.

The eggs are deposited immediately after fertilisation by the female and hidden singly under stones, etc.

There is no complicated metamorphosis, the young hatching out with the essential structure of the adult.

# Order Anaspidacea (Calman 9).

Diagnosis of the single Order is the same as that of the Division.

## Family I. Anaspididæ (Thomson 7).

The thorax is composed of eight distinct somites. The eyes are pedunculated. First antennæ of male without sensory modification. There is a well-developed antennal scale. The mandible has a cutting blade, a setose lobe and a molar expansion. The palp of the first maxilla is a nonsetose papilla. The first thoracic limb has gnathobasic lobes, a slender lamellar exopodite, and two branchiæ attached to the coxopodite. The anterior thoracic limbs are clearly composed of eight segments. The last thoracic limb is uniramous. The pleopods are all biramous with a small flabellate endopodite, except the fifth pair, which are without the endopodite.

## Genus 1. Anaspides (Thomson 7).

The thoracic segments are all nearly equal in length; the abdominal segments are slightly longer. The body is carried straight without any dorsal flexure. The antennal scale is shorter than the first two joints of the endopodite. The mandibular palp is without an exopoditic lobe.

The first thoracic limb has two gnathobasic lobes on the coxopodite. The sixth abdominal segment and the telson are as long as the two preceding segments. The telson is shorter than the uropods.

# A. tasmaniæ<sup>1</sup> (Thomson 7). Plate I, fig. 1.

The frontal margin of the head is produced into a conical projection, the sides and extremity of the cone being furnished with setæ (text-fig. 47). The eye-stalks do not project greatly beyond the lateral margins of the head. The body is carried flat and unflexed. On the head segment a median triangular piece is marked out by shallow grooves. The head segment is slightly longer than the first thoracic segment. The first thoracic segment is distinguished by the presence of two lateral sulci. The succeeding segments of both thorax and

## TEXT-FIG. 47.



Anaspides tasmaniæ. Head and eyes.

abdomen are sub-equal in length, but the sixth abdominal segment is considerably longer.

The first antennæ have the three basal joints short and stout; the internal flagellum consists of about twenty segments.

The otocyst is kidney-shaped.

The second antenna has a short scale, not reaching the top of the second joint of the peduncle.

The palp of the mandible is without an exopoditic lobe on its basal joint. The terminal segment is nearly half as long as the last but one.

The first maxilla has a small palp and three set near it.

<sup>1</sup> In the description of the species, those characters which have been mentioned or described in the diagnoses of the genera or families or in the anatomical part are only lightly touched upon, or in some cases not mentioned.

The second maxilla has the exopoditic lobe greatly reduced and fringed with a few minute setæ.

The first thoracic appendage has two gnathobasic lobes attached to coxopodite. The terminal segment, as in all living Anaspidacea, carries three enlarged setae, of which the middle one is the largest.

> TEXT-FIG. 48. 48.

Anaspides tasmania, J. A. First abdominal limb. B. Second abdominal limb.

There are two gills attached to the coxopodite of this limb, and of all the succeeding thoracic limbs except the last.

The seventh thoracic limb bears a small exopodite upon a distinct segment of the limb.

The fifth, sixth and seventh thoracic limbs of the female bear a small setose lobe on the inner face of the coxopodite.

The first abdominal appendage of the male possesses a spatulate endopodite furnished with a row of setæ proximally on its ventral internal face, and a pad of recurved hooks distally. The tip of the endopodite is simple.

The second abdominal appendage of the male possesses a biarticulate endopodite furnished on its internal face with a pad of recurved hooks. This pad is situated considerably below the joint separating the two segments of the endopodite. The terminal segment of the endopodite is without setæ or spines. There is no median spine on the sternum of this segment. There is a row of rather long setæ on the posterior dorsal margins of the fifth and sixth abdominal segments. The margin of these segments has a moniliform ornamentation owing to the bases of the setæ being raised.

The telson has the form shown in text-figs. 30 and 33A. It has a row of short setae confined to the posterior border.

The uropods have a short basal segment with a few lateral setæ. The exopodite has three enlarged lateral spines on its upper external margin. The setæ fringing the uropods are uniform in size and structure.

The adult animal may attain two inches in length.

The ground colour is straw yellow, but the skin contains a great number of black chromatophores disposed in a regular pattern.

Occurrence.—In isolated pools on and near the top of Mount Wellington, Tasmania; in the pools of the upper reaches of the North West Bay River on Mount Wellington, above the Wellington Falls; in the tarns on Mount Field, on the Harz Mountains and on Mount Read, West Coast of Tasmania. At an elevation of 2000 to 4000 feet.

# Genus 2. Paranaspides (Smith 12).

The first thoracic segment is longer than the two succeeding segments put together; the abdominal segments are much longer than the mid-thoracic segments. The body has a distinct dorsal flexure, the first abdominal segment project-

ing dorsally as a hump. The antennal scale is longer than the first two joints of the endopodite. The mandibular palp has a distinct setose exopoditic lobe. The first thoracic limb, besides the two gnathobasic lobes on the coxopodite, has the inner face of the first segment of the endopodite expanded into a setose lobe.

The sixth abdominal segment and the telson are together longer than the three preceding segments.

The telson is shorter than the uropods.

## P. lacustris (Smith 12). (Plate 11, fig. 2; text-fig. 1.)

The frontal margin of the head is produced into a conical projection, the cone being tipped with a bunch of setæ. The eye-stalks project considerably beyond the lateral margins of the head (text-fig. 4). The body is carried with a marked dorsal flexure. A triangular piece is not obviously marked out on the head segment, and the head segment is equal in length to the first thoracic. Lateral sulci are present on the first thoracic segment. The first thoracic segment is equal in length to the three succeeding segments. The abdominal segments are all longer than the mid-thoracic segments. The first antennæ have the basal segments elongated and rather slender; the internal flagellum consists of about twenty segments. The otocyst is oval.

The second antenna has a large scale, far exceeding in length the two joints of the peduncle (text-fig. 7).

The palp of the mandible may be four-jointed; it possesses a distinct exopoditic lobe, tipped with setæ, and the terminal segment is equal in length to the last but one (text-fig. 10).

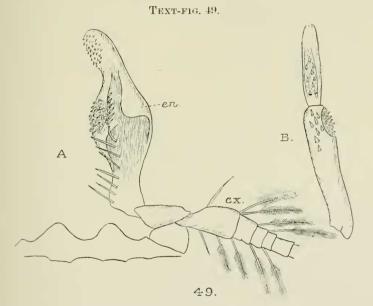
The palp of the first maxilla is larger than in Anaspides tasmaniæ, and there are no setæ near it (text-fig. 13).

The second maxilla has a fairly well-developed exopoditic lobe fringed with long setæ (text-fig. 16).

The first thoracic appendage has two gnathobasic lobes, and the third segment of the limb is expanded inwards into a lobate biting blade (text-fig. 19).

The thoracic limbs are built upon a similar plan to those of An aspides, but they are more slender and the setæ longer. The seventh thoracic limb has a small exopodite, but the segment bearing it is incompletely marked off from the other segments by a groove.

The first abdominal appendage of the male has a spatulate endopodite with an internal pad of recurved hooks, a



Paranaspides lacustris, J. A. First abdominal limb. B. Second abdominal limb. en. Endopodite. ex. Exopodite.

proximal row of setæ, and the tip is furnished with a number of short spines (text-fig. 49A).

The endopodite of the second abdominal appendage of the male has an external pad of recurved hooks near the top of the first segment, and the terminal segment carries a number of stout spines (text-fig. 49B). There is no median spine on the sternum of this segment.

There is a row of short spine-like setæ on the posterior dorsal margin of the fourth, fifth and sixth segments.

The telson has an elongated form with slightly concave sides. The posterior margin is produced into a number of spines of very unequal length (text-fig. 33B and 34).

The uropods have a short basal segment; the exopodite has six or seven stout spines on its external border. The other setæ fringing the nropods are uniform.

The adult animal may attain an inch in length.

The colour is transparent green, but with a few minute black chromatophores scattered about, chiefly on the lateral portions of the segments.

Occurrence.—In the littoral zone of the Great Lake of Tasmania, among weeds and stones. Elevation 3700 ft.

# Genus 3. Prieanaspides (Woodward 13). (Text-fig. 3.)

The first thoracic segment is much shorter than the others; the succeeding thoracic segments are sub-equal in size and the abdominal segments are on the whole equal to the thoracic. There is no dorsal flexure. The antennal scale is apparently just equal in length to the first two joints of the endopodite. The segment of the thoracic limbs immediately proximal to the knee-joint is expanded especially in the anterior limbs. The sixth abdominal segment and the telson are together a little longer than the two preceding segments. The telson is equal in length to the uropods.

## P. præcursor (Woodward 13).

The characters of this very important fossil are exhibited in text-fig. 3.

It is at once seen from these figures how close is the resemblance in all the essential characters between it and the living Anaspides. Similar transverse striations on the segments have been observed by Woodward in Palæocaris. With regard to the segmentation of the thoracic limbs it would appear that there were the typical three segments distal to the knee-joint and four segments proximal to it,

the separate segment bearing the exopodite having probably fused with the third segment, as in Koonunga and the posterior limbs of Anaspides. All the thoracic limbs except the last were apparently furnished with exopodites.

The abdominal appendages were probably very much as in An aspides, the exopodites being furnished with long, slender hairs.

For the determination of specific characters probably the hind segments, telson and uropods are most important.

The dorsal posterior borders of the third, fourth, fifth and sixth abdominal segments have a moniliform ornamentation showing where a row of spines was situated. The telson is elongated and bluntly rounded at the end. Its lateral borders are setose almost to the base, and at the posterior lateral angles a few longer setæ were present.

The uropods do not project further than the end of the telson. The outer ramus has a row of about seven short setæ on its outer border and two elongated spines at the line of segmentation near the tips of this ramus.

Length.-Largest specimen 57 mm. in length.

Occurrence. — In clay-ironstone nodules of the Coalmeasures near Ilkeston, Derbyshire.

# Family II. Koonungidæ (Sayce 10 and 11).

The thorax is composed of seven distinct somites, the anterior one being fused with the head. The eyes are sessile. First antennæ of male with sensory modification. There is no antennal scale. The mandible has a cutting blade and a setose lobe, but no molar expansion. The palp of the first maxilla is reduced, but distinct, and carries setæ. The first thoracic limb has a slender exopodite, but is without gnathobasic lobes. The thoracic limbs are composed of only seven segments. The last two thoracic limbs are uniramous. The pleopods are all uniramous, except the first two pairs in the male, which are modified as copulatory organs and retain their endopodites.

## Genus 1. Koonunga (Sayce 10 and 11).

The cephalic segment is about equal in length to the two following segments: there is a short transverse sulcus on each side at about the middle distance, posteriorly to which the margins are produced downwards and inwards. The thoracic and abdominal segments are all subequal in size, the sixth abdominal segment not being longer than the segments preceding it. There is no dorsal flexure. The telson is very short and does not equal in length the uropods. The basal joint of the uropods is nearly as long as the rami.

# K. cursor (Sayce 10 and 11). (Text-fig. 2.)

The frontal margin of the head is truncated and not produced into a projecting cone (text-fig. 50). There are no

TEXT-FIG. 50.

Koonunga cursor. Anterior region of head with sessile eyes.

setæ upon it. The minute sessile eyes are situated at the angles of the frontal margin. The body is carried flat and unflexed. There is no median triangular piece marked out on the head. The head segment is as long as the two succeeding segments and there is a marked transverse sulcus on each side. The succeeding segments, both thoracic and abdominal, are all subequal. The first antennæ has the first segment distinctly stonter and longer than the two succeeding segments. The inner flagellum is six-jointed, and in the male a peculiar sensory appendage is present, furnished with spiral hairs (text-fig. 51). The otocyst is circular. The second antenna is without a scale (text-fig 8).

The mandible is without a molar lobe, and the terminal

segment of the palp is much less than half as long as the last segment but one (text-fig. 11).

The first maxilla has a large palp, tipped with three setæ. The lower biting lobe has only three setæ. The exopodite of the second maxilla is not marked by the presence of any setæ. The first thoracic appendage is much stouter than the

TEXT-FIG. 51.

51.

ସ୍ଥ୍ୟର ଅଭିତ B

Koonunga cursor, S. A. First antenna, showing sensory appendage (ap.). B. Spiral sensory hairs from appendage.

succeeding limbs; it is without gnathobasic lobes or expansions.

The succeeding limbs are very similar to those of Anaspides save that the upper series of gills are much smaller relatively, and the last two limbs are without exopodites.

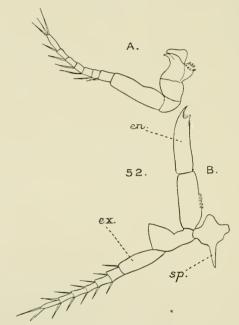
All the thoracic limbs consist of seven, instead of eight, segments.

The exopodites consist of far fewer segments than in Anaspididæ.

The first abdominal appendage of the male possesses a broad endopodite which ends in a curved hook and a broad blade; it is, in fact, definitely bifid. The pad of recurved hooks is borne on an internal projection (text-fig. 52A).

The endopodite of the second abdominal appendage of the male is two-jointed. The terminal joint is excavated at its tip and is clothed distally with very fine hairs. The pad of recurved hooks is situated internally on the proximal half of

TEXT-FIG. 52.



Koonunga cursor, J. A. First abdominal limb. B. Second abdominal limb. en. Endopodite. ex. Exopodite. sp. Spine on sternum.

the first segment. There is a large chitinous piece, with a posteriorly-directed spine, on the sternum belonging to this segment (text-fig. 52B). The posterior dorsal margins of the hind abdominal segments are without setae or moniliform ornamentation. There is a single large spine on each side on the posterior dorsal margin of the sixth abdominal segment.

The telson is short and obtusely conical, and its posterior

# ON THE ANASPIDACEA, LIVING AND FOSSIL. 567

and lateral margins are produced into a number of long stout spines of equal size. Between the spines are a number of short fine bristles (text-fig. 32).

The uropods have large basal segments furnished dorsally with three stout spines. The rami are short and truncated. The exopodite has about six long spines on its external border, and a number of long compound sette terminally, which become shorter as we approach the internal border. The sette clothing the endopodite are also much longer terminally than on the lateral borders.

The adult animal attains to about  $\frac{1}{3}$  inch.

The colour is dark, marbled brown; ground colour yellow, with numerous black chromatophores.

Occurrence.—From freshwater reedy pools beside a tiny runnel joining the Mullum-Mullum Creek, Ringwood, near Melbourne.

## Family III. Gampsonychidæ (Packard 5).

In this family may be included provisionally the three genera Gampsonyx, Palæocaris, and Gasocaris.

The thorax is composed of eight distinct segments of which the first is smaller than the rest. The succeeding segments, both thoracic and abdominal, are subequal in size, except the sixth which is somewhat elongated. An antennal scale was apparently present. All the thoracic limbs appear to have been biramous.

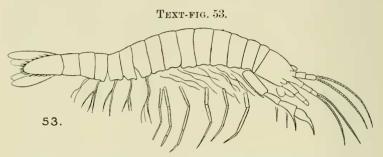
The body was carried straight without any flexure. The eyes were pedunculated.

# Genus 1. Gampsonyx (Jordan and v. Meyer 1) (=Gampsonychus = Uronectes).

The flagella of the first antennæ were apparently equal in length. The first thoracic limb was a powerful raptorial organ armed with curved claws. The endopodites of the hinder thoracic limbs were slender and much elongated.

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The telson was longer than the sixth abdominal segment. The abdominal appendages were apparently stout and flabellate.

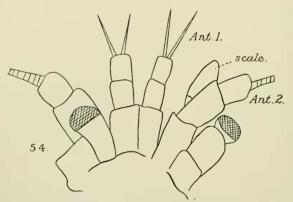


Gampsonyx fimbriatus. Reconstruction after Jordan and v. Meyer.

G. fimbriatus (Jordan and v. Meyer 1). (Text-fig. 53.)

The structure of the antennæ and eyes is shown in textfig. 54. The scale of the second antenna appears to have

TEXT-FIG. 54.

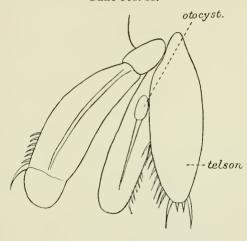


Gampsonyx fimbriatus. Head; after Fritsch. Ant. 1. First antenna. Ant. 2. Second antenna with scale.

slightly exceeded in length the first segment of the peduncle. The posterior thoracic and the abdominal segments have well-marked pleura,

The first thoracic limb is a powerful raptorial organ of the structure shown in text-fig. 53. The next two limbs were rather small and fairly stout, but the succeeding five thoracic endopodites are very long and slender. Fritsch denics that any exopodites were present, but it may well be contended that the fine strike figured by Jordan and v. Meyer springing from the bases of the thoracic limbs represent the hair-like setæ present on slender exopodites.

The abdominal appendages, according to Fritsch, are flabel-TEXT-FIG. 55.



55

Gampsonyx fimbriatus. Telson and uropod. After Fritsch. late in structure, but Jordan and v. Meyer made them out to be setose.

Fritsch gives a very finely detailed drawing of the telson and uropods (text-fig. 55).

The telson was an elongated oval, with setæ on its posterior lateral margins, and two long and two short setæ at the hind end. The outer ramus of the nropod was about equal in length to the telson, and had a row of six short setæ and one enlarged spine on its outer border. Fritsch figures a conspicuous sphere on the inner ramus which he interprets as an otocyst.

Occurrence.—In the Carboniferous of Saarbrück, Rhenish Prussia, and of Lebach, Bohemia.

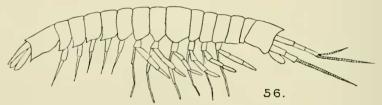
Genus 2. Palæocaris (Meek and Worthen 2 and 3).

The flagella of the first antennæ were unequal in size. The first thoracic limb was apparently not raptorial. The endopodites of the thoracic limbs were stont and short, exopodites elongated. The pleura of the abdominal segments projected backwards to end in a definite acute angle. The telson was shorter than the sixth abdominal segment. The abdominal appendages were slender, not flabellate.

# P. typus (Meek and Worthen 2 and 3). (Text-figs. 56 and 57.)

The chief interest of this fossil is, perhaps, to be found in

TEXT-FIG. 56.



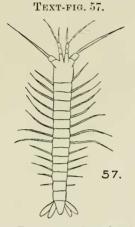
Palæocaris typus. Reconstruction after Packard. Lateral view.

the fact that Packard definitely demonstrates the presence of exopodites on the thoracic limbs. The eyes are unknown, but since in so many respects this fossil is close to Gampsonyx there can be little donbt that they were pedunculated. The thoracic limbs, if we can trust Packard's restoration, were all similar and biramous.

The telson was broad and short and apparently clothed with a uniform border of setæ. The uropods projected beyond the end of the telson and were also apparently clothed with uniform setæ.

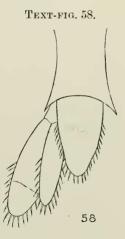
In certain respects Meek and Worthen's figure (text-fig. 57) in dorsal view of P. typus is more interesting than

Packard's obviously diagrammatic restoration. The specimen is flat and resembles to an extraordinary degree the dorsal view of Præanaspides given by Woodward (text-fig. 3 B).



Palæocaris typus.

Reconstruction after Meek and Worthen. Dorsal view.



Palæocaris typus. Telson and uropod. After Packard.

We see also in this figure the limbs spread out laterally in the exact position assumed by Anaspides when walking.

Length.-78 inch.

Occurrence.-In clay-ironstone concretions in lower Coalmeasures of Mazon Creek, Morris, Illinois.

Woodward describes another species, P. Burnettii, measuring 30 mm. from the middle coal-measures of Irwell, Lancashire. In this species he describes the transverse striæ on the segments which he afterwards observed in Præanaspides.

# Genus 3. Gasocaris (Fritsch 17).

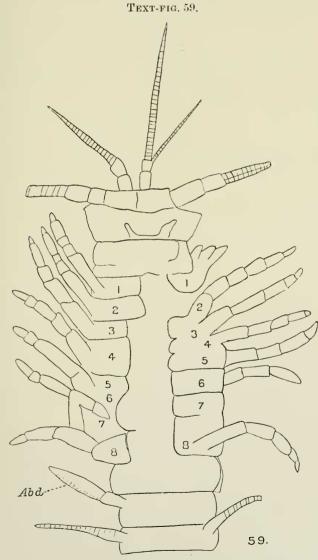
The flagella of the first antenuæ are unequal in size. All the thoracic limbs are similar, rather short and stoutly built (without exopodites according to Fritsch). The telson is rather shorter than the uropods. There is a row of setæ on the posterior dorsal margin of all the thoracic and abdominal segments. The body is broad anteriorly, tapering considerably toward the hinder end. The abdominal limbs are stout, but annularly segmented.

# G. krejcii (Fritsch 17). (Text-figs. 59, 60, and 61.)

Fritsch establishes beyond doubt the pedunculated nature of the eyes and the structure of the first and second antennæ. In his restoration, however, he makes the two flagella of the first antenuæ equal in size, which is contradicted by his figure of an actual specimen in ventral view (text-fig. 59). The scale of the second antenna seems to have reached the top of the peduncle on which the flagellum is inserted. With regard to the segmentation of the body his reconstruction is impossible to reconcile with the ventral view of an actual specimen. In the reconstruction he makes, besides a narrow head-segment, only six thoracic segments. In the ventral view, reproduced here, it is easy to make out eight free thoracic segments with limbs, and a broad segment in front to represent the head, and this structure would bring the specimen into line with the other Anaspidacea. The thoracic limbs, as reconstructed by Fritsch, are all similar, being rather short and

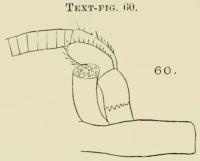
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stout and apparently without exopodites, though with regard to this latter point we may well keep our judgment suspended,



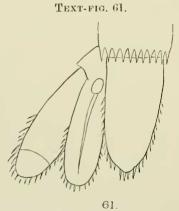
Gasocaris krejcii. Ventral view. Adapted from Fritsch. 1–8. Thoracic segments. *Abd*, Abdominal appendage.

owing to the difficulty of making out the exopodites in even the best preserved fossil Syncarida. The abdominal appendages



Gasocaris krejcii. Compound eye and second antenna. After Fritsch.

appear to have consisted of a stont outer ramus, segmented in the annular way characteristic of such a form as Anaspides. I cannot observe in Fritsch's figures of actual specimens any



Gasocaris krejcii. Telson and uropod. After Fritsch.

trace of endopodites, though Fritsch in his reconstruction figures the appendages as consisting of endopodite and exopodite of equal length. It appears more probable that the endopodite was the reduced flabellate structure which we know in the living Anaspides.

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The telson is ovate or conical, with a border of short uniform setæ round the posterior three quarters of the margin. The uropods projected slightly beyond the telson and were fringed with uniform setæ. Fritsch figures an otocyst at the base of the inner ramus.

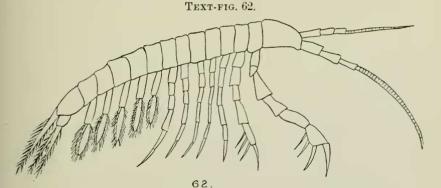
Length.—About 13 mm.

Occurrence.—In Coal-measures of Nyran near Pilsen; in older strata than those in which Gampsonyx occurs.

Genera of doubtful position.

Genus Acanthotelson (Meek and Worthen 2).

Two species are described, A. stimpsoni and A. in-



Acanthotelson stimpsoni. Reconstruction after Packard. Lateral view.

æqualis. Packard gives a restoration of the genus. He figures besides a head segment, seven thoracic and six abdominal segments and a telson. The eyes are unknown. The first antennæ had a three-jointed peduncle and a single flagellum, according to the restoration, though it appears that it may have had two. The second antenna was apparently without scale. The seven thoracic limbs were long, fairly stout, and without exopodites. The first two limbs were raptorial iu structure and furnished with long spines on the

penultimate joint. The abdominal appendages had a long basal segment and a terminal flabellate segment clothed with long seta.

The telson was an elongated pointed spine fringed with long setæ. The uropods, which consisted of external and internal rami, were also long and pointed, and they were fringed with long setæ.

Occurrence.-Coal measures of Illinois.

### Genus Nectotelson (Brocchi 19).

N. rochei from the Permian of Autun, France. Only very badly preserved specimens known.

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## EXPLANATION OF PLATES 11 AND 12,

# Illustrating Mr. Geoffrey Smith's memoir on "The Anaspidacea, Living and Fossil."

### PLATE 11.

FIG. 1.—Anaspides tasmaniæ. Dorsal view of a very large specimen. Natural size, in normal position for running.

FIG. 2.—Paranaspides lacustris. Lateral view. Natural size, in position for running or swimming.

FIG. 3.--Shoot of the liver-wort, Yungermannia, with two eggs of Anaspides tasmaniæ.  $\times$  5.

## PLATE 12.

FIG. 1.—Transverse section through otocyst of Anaspides,  $\times$  50. ec, ectoderm; *n*, antennulary nerve; *m*, muscle; *r*, setose ridge.

FIG. 2.—Portion of blood-forming organ of Anaspides, showing mitoses and detached corpuscles.

FIG. 3.—Transverse section through the cardiac portion of stomach of Anaspides. C and D, lateral ridges; E, dorsal median ridge; H, ventral ridge.

FIG. 4.—Transverse section through the alimentary canal of Anaspides, where the first diverticulum (div. 1) opens into the mid-gut. The section is not quite transverse, so that the opening is only seen on the right side. *B*, lateral chitinous ridge of pyloric division of the stomach extending into mid-gut; *b. m.*, basement membrane of mid-gut. *Div.* 1, first diverticulum, showing crowded nuclei and mitoses.

FIG. 5.—Transverse section through anterior portion of mid-gut, showing basement membrane (b. m.), and special gland-cells (g.).

FIG. 6.—Section through a special gland of mid-gut, showing flattened nuclei of gland-cells.

FIG. 7.—Section through wall of posterior part of mid-gut, showing absorptive layer (m.), basement membrane (b. m.), and submucosa (s. m.).

FIG. 8.—Transverse section through a liver tube of Anaspides, unfed condition. g, special gland-cells.

FIG. 9.—Transverse section through a liver tube, full-fed condition with fat vacuoles in cells.

FIG. 10.—Transverse section through external duct of maxillary gland.

FIG. 11.—Section through a more internal part of gland.

FIG. 12.—Section through a more internal secretory part of gland.

FIG. 13.—Section through a portion of end-sac.

FIG. 14.—Longitudinal section through a piece of ovary of Anaspides, showing two large ova, small ova lying in the lobes on the right, and the trophic cells (*tr.*) on the left.

FIG. 15.—Transverse section through testis of young Anaspides, showing trophic cells (*tr.*), primary (*sp.* 1), and secondary spermacytes (*sp.* 2), and spermatozoa (*spt.*).

FIG. 16.—Upper portion of vas deferens, with albuminous part of spermatophore in lumen, and trophic cells (*tr.*) surrounding it.

FIG. 17.—Section through the supporting tissue of glandular appearance which surrounds the ducts of the spermatheca, and is also present in the labrum.